10.—Mammal remains from the upper levels of a late Pleistocene deposit in Devil's Lair, Western Australia

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Abstract

This paper reports on continuing investigations of the fossil mammal fauna from the sandy deposit in Devil's Lair, a small cave in the extreme south west of Western Australia. Excavations in 1972 and 1973 produced a substantial sample of bone fragments about 12 000 to about 19 000 years old, and a much smaller sample about 19 000 to about 25 000 years old. Most of these remains appear to be of animals eaten by humans occupying the cave intermittently, perhaps in small groups.

Neither Dingo nor any of the large extinct Pleistocene marsupials is included among the 35 mammal species so far detected in the deposit. Between 19 000 years ago and about 12 000 years ago most species are present at all levels, but at least one trend in the relative abundance of the more common species is suggested, and seems to be clearest about 12 000 years ago. An improved list of the modern mammal fauna of the district is presented and compared with the fossil fauna; there appears to have been a considerable decrease in species diversity since the Pleistocene. Species lost have mainly been those adapted to shrub formations or woodlands, whereas species adapted to forest have persisted. These changes are the culmination of the above trend in relative abundance. Two possible causes are discussed: the effects of the glacioeustatic rise in sea level acting alone by changing the extents of different habitats, or acting in conjunction with local climatic changes such as an increase in effective rainfall.

Contents

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Introduction

Excavations in Devil's Lair, a small cave in aeolian calcarenite in the extreme south west of Western Australia, were begun in 1955 by E. L. Lundelius with the object of learning something of the prehistoric mammal fauna of the region. After various unsystematic extensions of these initial excavations, and after realisation that the deposit included an archaeological component, the Western Australian Museum began a series of systematic excavations, to be spread over a number of years. In preparation for this series, a reserve including the cave has been vested in the Museum, and a steel mesh fence erected across the cave mouth. Thus it seems justifiable to leave excavations open from field season to field season and to extend them as opportunity offers.

The deposit yields vertebrate remains in abundance as well as substantial numbers of artifacts, so that a few excavators working for some days produce material requiring many months of preparation and study. The intention is to report progress at intervals, leading to a summary in due course. Present indications are that several more years' work must precede any such summary.

This paper presents an analysis of animal remains recovered from excavations made in February 1972, and March 1973. A general report on the first of the series of systematic excavations, made in December 1970, has been issued by Dortch and Merrilees (1972), and a report dealing mainly with the archaeological component from the 1972 excavations has been issued by Dortch and Merrilees (1973). Dortch (1974) has discussed archaeological aspects of the 1973 excavations, and Glover (1974) has discussed geological aspects of the material of some of the articrafts recovered. Davies (1968, and Appendix to Dortch and Merrilees, 1973) has described human incisor teeth. Other specialist reports are in preparation.

We follow the mammal species concepts and names of Ride (1970).

Devil's Lair lies about 5 km from the sea on the eastern side of a ridge. The vegetation of the region has been described by Smith (1973). The western slope of the ridge, which is exposed to the prevailing westerly winds off the southern Indian Ocean, is covered by an open heath in which *Acacia decipiens* is the principal species. Near the sea *Olearia axillaris* and *Scaevola* spp. are also important components. Where some shelter exists on the top of the ridge open scrub,

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low woodland, or low open forest may occur. Peppermint (*Agonis flexuosa*) or Jarrah (*Eucalyptus marginata*) are usually the principal species in these formations. On the eastern slopes of the higher parts of the ridge open forest quickly gives way to high open forest in which Karri *(E. diversicolor)* grows in fairly pure stands. Devil's Lair lies in the middle of one such belt of Karri forest which stretches for some 20 km from Calgardup Brook in the north to Turner Brook in the south. On the inland (eastern) side of the Karri is an extensive open forest of Jarrah and Marri (*E. calophylla*) continuing in to the valley of the Blackwood River some 10 km to the east, and for a much greater distance to the north east. Only about 3 km to the east of Devil's Lair is McLeod Creek along which dense shrub vegetation grows.

The 1972 and 1973 Excavations

Several trenches were opened in Devil's Lair during the 1972 and 1973 field seasons, for reasons given by Dortch and Merrilees (1973), who show the positions of these trenches in the cave and briefly describe the geological setting. Very few animal remains were recovered from Trenches 3 and 4. This paper is based almost entirely on specimens recovered from Trench 6 and from a complex of trenches, Nos 2, 5, 7 and 8 (7 and 8 with subdivisions) of our field and laboratory records.

Figure 1   Plan of trenches 2,5,7,8 in Devil's Lair
Nominal east face of Trench 8 is wall of cave

The relations of Trenches 2, 5, 7 and 8 to one another and their dimensions are shown in Figure 1. Trench 6, oriented similarly to Trench 5 but 1½ m long by 1 m wide, was close to the cave wall about 3 m south west and slightly down slope from Trench 5. All depths have been recorded below the same arbitrary datum mark on the wall of the cave, and thus may be compared directly.

The various trenches have been excavated to different depths, which are recorded in the tables in Appendix 1. Trenches 7 and 8 have been excavated only to shallow depths as yet, Trenches 5 and 6 to intermediate depths, while Trench 2 is deepest, but no trench has yet reached the bottom of the deposit, and steel rods driven down from the bottoms of Trenches

6 and 2 show at least a metre thickness of deposit below each.

Nature and age of the deposit

Much of the Devil's Lair deposit is made up of grains of quartz to some extent coated and lightly cemented by calcite. As a result excavation is usually easy, yet vertical excavation walls remain stable for years. The colour of the deposit varies. The sandy portions show various shades of orange and brown, but there are paler coloured bands and irregular masses which have been more or less strongly lithified by calcareous cement, while the uppermost layer is black. Flowstones, stalagmites and other almost entirely calcareous materials, crystalline at the macroscopic level, are interbedded with the sandy material. Calcareous solutions drip from the roof of the cave and permeate the deposit during the wetter months of the year at present, and presumably always or usually have done so, and have been responsible for patches and zones of lithification.

During the drier months of the year, the sandy portions of the deposit become sufficiently dry to pass easily through our screens, but enough moisture is present at some times of the year to support the growth of tree roots. These appear to be associated in some way not at present understood with bands and pockets made up entirely or partly of gypsum.

There are lenticular inclusions of ashy appearance, which we have interpreted as hearths, particularly near the top of the deposit. Charcoal is widely dispersed, usually in small pieces not exceeding a few millimetres across. Fragmented bone is also widely dispersed through the deposit, and there is a small but significant proportion of rock fragments foreign to the cave. Large and small rock fragments, mainly of calcrete, much or all of which could be derived within the cave, are abundant in places, and broken stalactites also occur.

Detailed analysis of the sediments is in progress, and will be reported in due course by M. L. Shackley.

In order to avoid prejudice to later determinations of stratigraphic equivalences throughout the cave, we have used field designations for the "natural" stratigraphic divisions or arbitrary depth determined units of excavation ("spits") differing from trench to trench or field season to season. These field designations are recorded not only in our field notes but also on specimen labels and in the Museum catalogues, and to some extent are reproduced in the Appendix 1 tables.

However, we have attempted to group and analyse our data in terms of the major stratigraphic divisions recognised by Dortch and Merrilees (1973), and comparison of their stratigraphic sections and names with ours may be made readily even though we have modified the names slightly in some cases. A stratigraphic section revealed in the southwestern walls of the adjacent Trenches 5, 2 and 8₂ is represented in
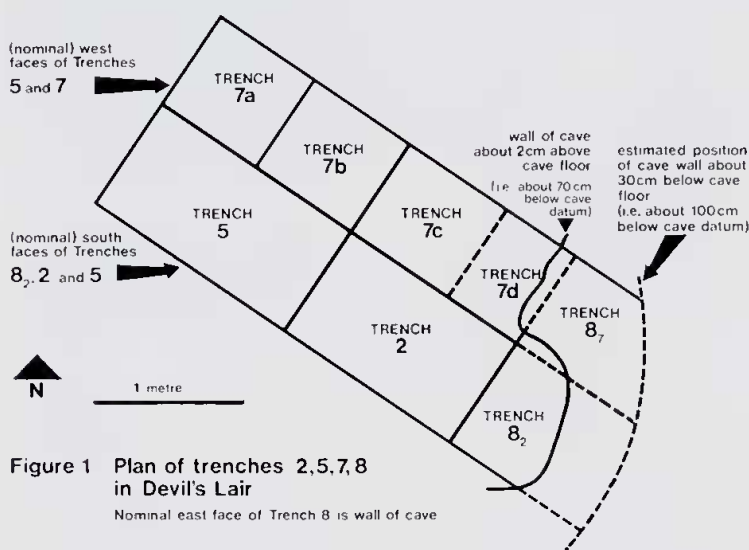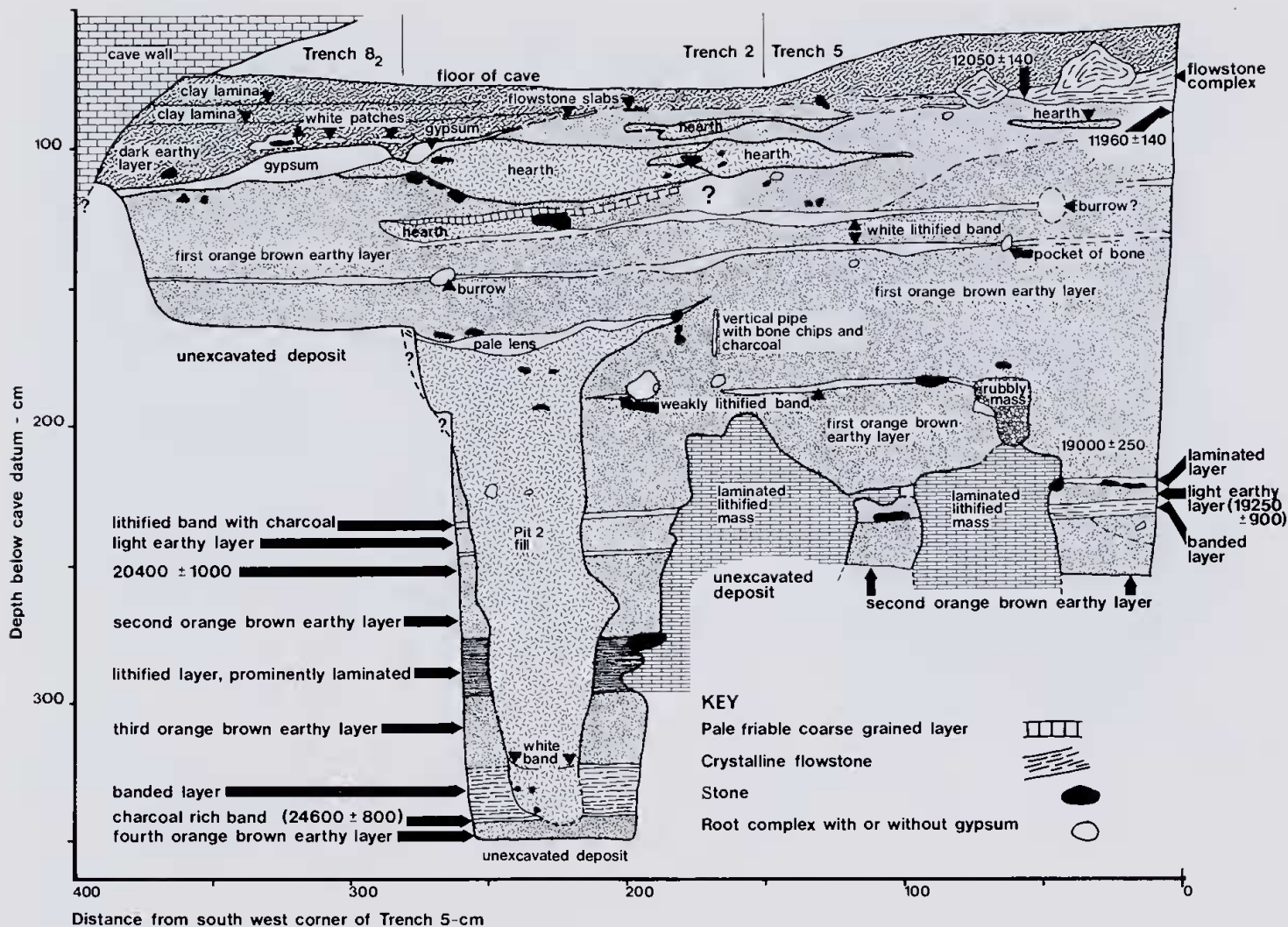
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DEVIL'S LAIR : (NOMINAL) SOUTH FACES, TRENCHES 8₂ 2 5

Figure 2.—Section revealed by excavations to 1973, south faces of adjacent Trenches 8₂, 2 and 5.

Diagram labels (stratigraphic section):

Depth below cave datum - cm (100, 200, 300)

cave wall; Trench 8₂; Trench 2 | Trench 5; floor of cave; clay lamina; clay lamina; white patches; gypsum; flowstone slabs; dark earthy layer; gypsum; hearth; hearth; hearth; hearth; 12050 ± 140; flowstone complex; hearth; 11960 ± 140; first orange brown earthy layer; burrow; burrow?; white lithified band; pocket of bone; first orange brown earthy layer; unexcavated deposit; pale lens; vertical pipe with bone chips and charcoal; weakly lithified band; first orange brown earthy layer; rubbly mass; 19000 ± 250; laminated layer; light earthy layer (19250 ± 900); banded layer; laminated lithified mass; laminated lithified mass; unexcavated deposit; second orange brown earthy layer; second orange brown earthy layer;

Pit 2 fill

lithified band with charcoal; light earthy layer; 20400 ± 1000; second orange brown earthy layer; lithified layer, prominently laminated; third orange brown earthy layer; banded layer; charcoal rich band (24600 ± 800); fourth orange brown earthy layer; white band; unexcavated deposit

KEY
Pale friable coarse grained layer
Crystalline flowstone
Stone
Root complex with or without gypsum

Distance from south west corner of Trench 5-cm (400, 300, 200, 100, 0)

Figure 2; for convenience this has been called the "south" face, though its trend is actually N 123°. Dortch (1974) illustrates the shallow north face of Trench 7, opposite that shown here in Figure 2.

Radiocarbon dates on charcoal samples from various parts of the deposit have been reported by Dortch and Merrilees (1973). These dates have been included in Figures 2, 4, 5 and in the Appendix 1 tables in their relative stratigraphic positions. They show that the uppermost major stratigraphic unit ("dark earthy layer") is less than 12 000 years old by an amount not at present known, and that the other major stratigraphic units so far excavated extend back in age from about 12 000 to about 25 000 years before the present. This is the period covered in the present report. Dortch and Merrilees (1973) suggest that the bottom of the deposit represents a time more than 30 000 years B.P.

Procedures

Excavation was made by trowel and brush, the excavated material being sieved with "coarse" and "fine" screens (5 mm and 3 mm square openings respectively), with random samples passed additionally through screens of 1¼ mm square openings (our "finest" screens). The material remaining on the screens was examined at the site, in the cave in 1972 and in full daylight in 1973, and bone and artifacts removed. The residue was thrown away after two screeners were satisfied that sorting was complete. Some material may have been overlooked in sorting, especially in 1972 when artificial light was used. Checks on randomly selected samples of material passing through the fine screens suggest that little macroscopically identifiable material was lost.

Samples for pollen analysis, radiocarbon dating, and sediment analysis were taken as described by Dortch and Merrilees (1973).

The bone recovered was well preserved, with details such as muscle scars, foramina or tooth cusps sharply defined, though concealed by calcareous coatings in some cases, and showing brown coloration in most. Calcareous coatings were often easily removable with brushes or steel dental probes, though in some cases the coatings were well cemented and required considerable pressure to flake them off. Even so, the tooth and bone beneath generally suffered little damage and very little acid preparation of specimens was necessary.
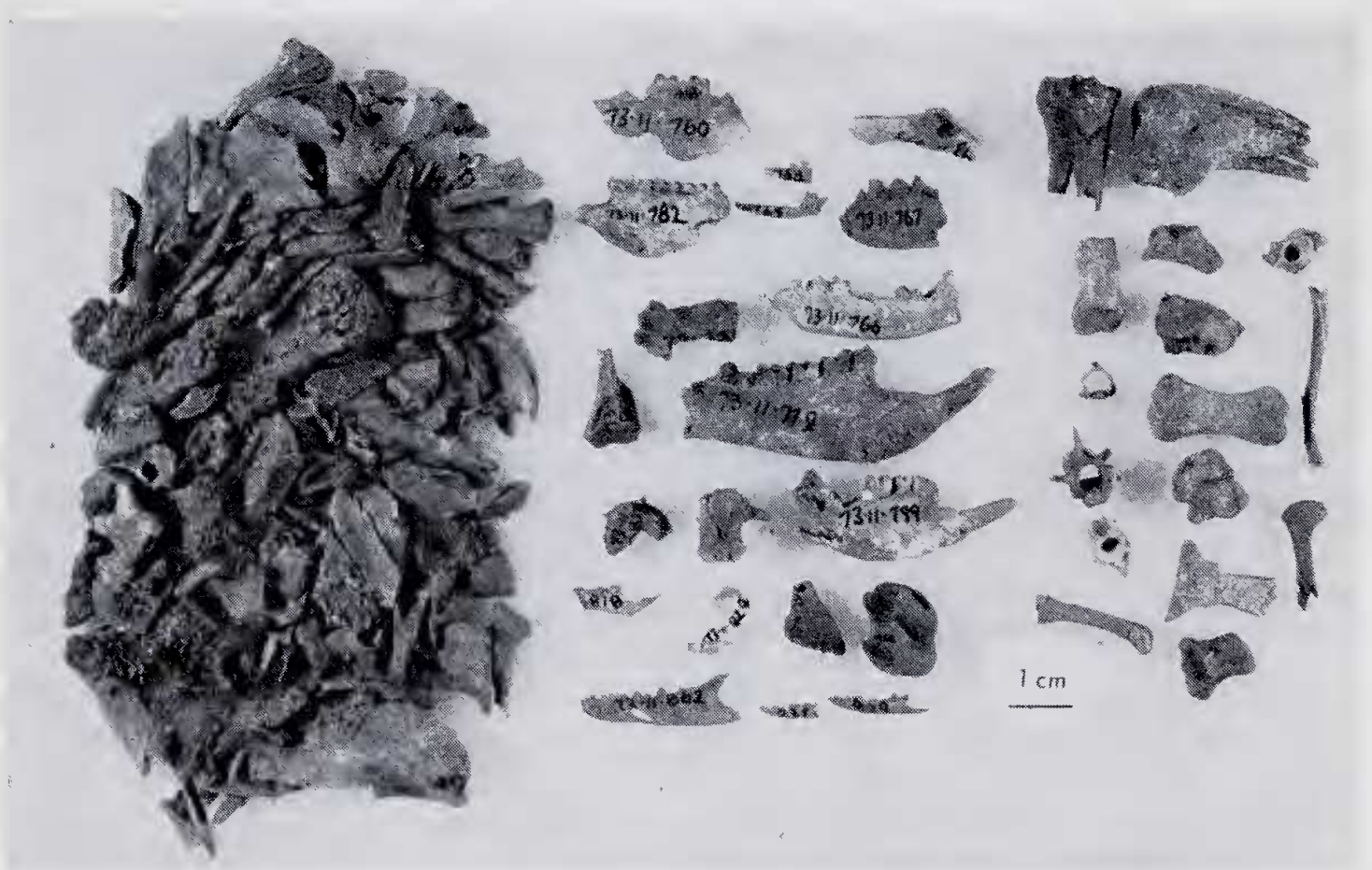
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Figure 3.—Typical bone fragments from Devil's Lair, excavated from unit O in upper middle subdivision of first orange brown earthy layer in Trench 8_2, 136-149 cm below cave datum. This is not the whole sample. *Left:* fragments which for practical purposes are not identifiable. *Centre:* identified and catalogued fragments typical of those on which this paper is based. *Right:* fragments which could be, but which for lack of time have not been identified.

A conspicuous feature of the bone samples recovered from Devil's Lair, unlike those from some other caves nearby, was fragmentation, as illustrated in Figure 3. Bone fragmented to about the same degree was abundant at most stratigraphic levels, so much so that for practical reasons a selection had to be made of what was to be identified and studied. All fragments bearing teeth or with tooth sockets, and all isolated teeth were included, and all clearly recognisable fragments of calcaneum, femur, pelvis, humerus and scapula of mammals, and vertebra and femur of lizards. Any of the highly characteristic fragments (such as the tibiotarsus in the case of birds or vertebra in the case of snakes) representing the lower vertebrates also were included. Other material was excluded from our analysis, even in cases such as the tibia in macropods, which is readily identifiable, in order to keep the findings comparable from taxonomic group to group, especially among the mammals.

From the material identified, estimates were made of the minimum number of individuals of each taxon represented in each stratigraphic subdivision or arbitrary spit excavated from each trench. At least one fragment representing each such individual was given a catalogue number and appropriate catalogue entry, but it was not feasible so to catalogue every fragment recovered. Identified but uncatalogued fragments

all have been stored with their catalogued counterparts, and the remaining unidentified fragments from each subdivision or spit have been stored with some catalogued specimen from that subdivision. Thus any specimen retrieved from the screens, whether or not formally catalogued, is available for further study.

Except for bone artifacts (stored in the archaeological collection) and human skeletal remains (so far only two isolated incisor teeth, stored in the anthropological collection) all bone and other biotic material from the Devil's Lair excavations is stored in the Western Australian Museum palaeontological collection. Catalogue numbers for vertebrate material from the 1972 and 1973 excavations are as follows: 73.7.148-1006, 73.8.1-998, 73.9.1-1156, 73.10.1-1452, 73.11.1-1059, 73.12.1-512, 74.5.32. Thus 6 037 specimens have been catalogued. We have not counted identified uncatalogued specimens, but they probably amount to several thousands while unidentified fragments amount to tens of thousands. Dortch and Merrilees (1972) reported upon 1 486 catalogued vertebrate specimens.

In making the estimates of minimum numbers of individual animals shown in Appendix 1 tables, we regard each "natural" stratigraphic unit or arbitrary subdivision or spit excavated in each trench as an entity separate from every other such entity. In fact, many of these units were merely portions of a continuum. Even in

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some cases where clear cut lithological differences appeared to mark breaks in the continuum, these differences may have arisen in various secondary ways within a continuous sediment. In other cases, bone fragments left lying on a surface marking a significant pause in sedimentation may have been mixed with bone fragments from the stratigraphic unit below them by trampling, digging or other processes both natural and artificial. Furthermore, it is likely that the bones of any individual would be scattered over an appreciable lateral area, whatever agent was bringing the bones into the cave, and that frequently this lateral scattering would be beyond the confines of our trenches.

Thus it is to be expected that different parts of the same skeleton would turn up in different stratigraphic units and different trenches, and would not normally be recognised as parts of the same animal. Thousands of individuals were represented in most of our major trenches, so that averaging effects probably were operating, but even so, the excavating and counting procedures we adopted may have led us to overestimate the minimum numbers of animals represented in the deposit.

We estimated minimum numbers of individuals in each stratigraphic unit by first assigning each identifiable fragment to a species and then determining for each species sample which anatomical element was most numerous. We then considered each other anatomical element from the point of view of whether it could represent an individual additional to those previously counted. An example is given in Appendix 3 for *Sminthopsis murina*, and other authors (e.g. Bökönyi 1970, Chaplin 1971) have given other examples of this method.

Criticisms of such methods of attempting to quantify animal bone samples have been made by Uerpmann (1973), Perkins (in Matolcsi 1973) and others. Uerpmann advocates weighing all the bones of each species in order to estimate the meat they represent, but it would not be feasible for us to separate all the fragments found into species. Perkins suggests that each bone found should be taken to represent a separate individual unless the time range of the sample is known, there was a high rate of preservation of bone and there was virtually complete recovery from the excavation. All these conditions are met by our sample, and we would probably greatly overestimate the animals actually contributing to the sample if we accepted even each identifiable fragment as representing a different individual, ignoring unidentifiable fragments.

Thus we have adhered to the usual "minimum number" estimate, recognising that this is only a comparative figure, possibly differing quite substantially from the number of animals actually contributing to the sample. In order to gauge the degree of overestimation we made the investigations reported in Appendix 3. We conclude that our methods may lead to overestimation which becomes more likely with increasing size of the animal concerned and decreasing thickness of the excavation unit sampled.

Stratigraphic reliability of the sample

We have suggested that the estimates given in the Appendix 1 tables of minimum numbers of individuals involved in our sample must be used with caution on statistical grounds. There are in addition some stratigraphic considerations which suggest caution in the use of these estimates.

We are not yet able to quantify the effects of deliberate digging by human beings on vertical mixing of the sample nor of digging or reworking by other agencies. But it is clear that there was much digging in the deposit by the human occupants of the cave.

The digging in prehistoric time of the large, steep sided Pit 2 must have resulted in a substantial number of bone fragments being brought up from depths of as much as 3 m and distributed over the floor from which Pit 2 was dug. See Figure 2. Dortch and Merrilees (1973) reported the finding of the lower part of Pit 2, but were unable to trace the upper part of this pit. Subsequent examination has revealed the top and upper western wall of the pit. The "pale lens" shown in Figure 2 at a depth of about 170 cm in Trench 2 is interpreted by us as occupying the slightly slumped top that might be expected to result from the filling of an open hole by sediment and occupational *débris*. The stratigraphic implications of this interpretation are (a) that Pit 2 was dug from a floor (not so far recognised in our excavations) at a depth of about 150 cm, i.e. at an intermediate depth in first orange brown earthy layer and (b) that Pit 2 fill is stratigraphically equivalent to an intermediate depth in undisturbed first orange brown earthy layer. However, it is possible that the pit was refilled with the original material by the people who dug it because otherwise it would have been a hazard in an unlit cave.

There is probably confusion in our sample from some intermediate depth in what has been labelled "first orange brown earthy layer" in Trenches 2 and 5, and possibliy also in Trenches 7 and 8, of old bone fragments brought up from Pit 2 with the bone fragments representing the then current human occupation of the cave. It is even possible that this contamination by older *débris* extends as far as Trench 6, about 3 m south of the known boundary of Pit 2 in Trench 2.

During the 1972 excavations, it took some time to appreciate the full extent of hearth and pit digging illustrated here in Figure 2, and Dortch and Merrilees (1973) draw attention to the resulting stratigraphic confusion of samples from the large Hearth 1 in Trench 6 and the underlying brownish earthy layer into the top of which Hearth 1 was dug. In our appendix tables, this confusion is noted. There must be some similar confusion in the upper parts of Trench 5 which has gone unremarked in our appendix tables because it was not recognised in the field and its extent was not recorded. In these cases the mixing is not likely to involve bone fragments of very different ages.

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We believe that specimens 73.9.1066 (recorded as coming from Pit 2 fill), 73.9.1004, 1005 (recorded as coming from banded layer) and 73.9.1039, 1040, 1048, 1049 (recorded as coming from fourth orange brown earthy layer), from the lower parts of Trench 2 represent the same animal. It is possible to match broken edges in two specimens, the various parts look alike in texture and colour, all fragments represent an extremely young animal, and some bones are unbroken and clearly associated with one another, a very unusual occurrence in Devil's Lair. The animal concerned was a young individual of *Bettongia lesueur* (not *Pseudocheirus peregrinus* as recorded by Dortch and Merrilees 1973 p.99). The stratigraphic implication is that the exact boundaries of Pit 2 were uncertain, as suggested by dotted lines in the section drawings, Figure 2 herein and Figure 5 of Dortch and Merrilees (1973).

It is possible that other material from the bottom of Pit 2, contemporaneous with an intermediate level in first orange brown earthy layer, has been confused with older material from banded layer or from fourth orange brown earthy layer, and we do not know the extent of any such confusion. However, because the charcoal rich band from which a charcoal sample was taken for dating is very well defined and clearly is not present in Pit 2 fill, we consider that the date recorded (24 600 ± 800 yr B.P., SUA-31) reliably represents undisturbed material. We believe that four quartz and some probable calcrete artifacts catalogued as B1545 and B1546 from below this charcoal rich band also came from undisturbed material.

Two detached lumps of flowstone (now in the geological collection of the Western Australian Museum under catalogue numbers 13324, 13325) were found near the western face of Trench 7a in its uppermost part, resting on thick macrocrystalline flowstone obviously in its undisturbed position (flowstone D, illustrated in Figure 3 of Dortch 1974). These lumps were upside down. The stratigraphic implication is that they and possibly some or all of the bone fragments and other material from the uppermost western part of Trench 7a are disturbed and of unknown age. We suspect that they represent spoil from the unsystematic excavation of the upper part of Trench 2 (shown by Dortch and Merrilees 1972, Figure 1, as "Small Excavation"), which was made before the present systematic series began in 1970, or that they are spoil from ancient digging.

From the presence of an unbroken thin lithified band (labelled B in our field records) in the uppermost eastern part of Trench 7a and extending into Trench 7b and 7c, we are satisfied that most of the dark earthy layer in Trench 7 is undisturbed, as illustrated in Figure 3 of Dortch (1974). Nevertheless, some (probably most) of the animals recorded for dark earthy layer in Trench 7 in Appendix 1 tables represent disturbed material of unknown stratigraphic origin. This disturbance probably affected dark earthy layer in Trench 5 but was not detected during excavation. Therefore we make no inferences from the fauna recorded from dark earthy layer.

Source of the bone sample

Dortch and Merrilees (1973) and Dortch (1974) show that humans occupied Devil's Lair at times, and it is possible that much of the bone sample here discussed represents discarded remnants of human meals. A small proportion of the bone fragments recovered are charred, possibly in the process of cooking carcases, or possibly from being discarded into camp fires, as mentioned by Hammond (1933) for modern Aborigines. Charring has been noted affecting the following taxa in Devil's Lair; the catalogue number in brackets represents one example:— *Dasyurus* (73.8.294), *Isoodon* (73.8.359), *Perameles* (73.8.448), *Potorous* (73.12.173), *Bettongia penicillata* (73.10.1264), *B ? lesueur* (73.12 154), *Petrogale* (73.9.1151), *Macropus fuliginosus* (73.9.783), *Setonix* (73.12.182), *Rattus fuscipes* (73.11.60), lizard (73.8.821), snake (74.5.32).

Presumably marrow would have been eaten by ancient Aborigines, as by other people (e.g. modern American Indians—Neumann and DiSalvo 1958). Also it is possible that small bones were attractive as food items to a people accustomed to using their teeth as vigorously as described by Campbell (1939) for modern Aborigines and by Neumann and DiSalvo (1958). But it is difficult to account for the extreme fragmentation of practically all bones in the sample (see Figure 3) unless food preparation methods then in use included systematic pounding of the carcases before or after cooking, as described by Gould (1968a) for modern inland Aborigines. Tedford (in Gould 1968b) comments on fragmentation and charring of bones from an inland archaeological site, suggesting that pounding of food animals is a long standing practice of these inland peoples. Brain (1970) suggests that extreme fragmentation of bone in a deposit, and Gorman (1971) that fragmentation with some charring, is a hallmark of human contribution.

Lundelius (1966) believed that fragmentation of bone, presence of predator remains, and bone bearing coprolites together indicated that a bone bearing deposit had been accumulated by that predator, in this case *Sarcophilus*. Indeed, the name "Devil's Lair" was conferred on the site because of his belief. Much of the bone from our excavations is reminiscent of that recovered from modern *Sarcophilus* leavings described by Douglas, Kendrick and Merrilees (1966).

It is possible that while primary fragmentation of our bone sample was the work of Aborigines, secondary fragmentation resulted from devils working over the leavings of human beings after (or perhaps even during) human occupation of the cave. Devils now live successfully in close contact with human activities in parts of Tasmania (Guiler 1970). They may long have done so, and indeed may have occupied the place later held by dogs in Aboriginal camps. If dogs had been living in Devil's Lair it seems very probable that some remains would have been detected.

Thus we cannot be sure of how much of the bone in our sample represents human meals, but from the charring of some of it and the form of bias demonstrated below in the remains of

Macropus fuliginosus, we are confident that some of it does. Adult *M. fuliginosus* are too large to be killed by devils; however, some remains of this species may have been brought into the cave as carrion. The presence of shell fragments of mussel and the eggs of emus (Dortch 1974) marine shell (Dortch and Merrilees 1972) and the single fish vertebra (73.11.177) which is the basis for the fish entry in Trench 8₇ in the appendix tables, also point to man as a contributing predator. No other single predator species is likely to have sampled the wide range of habitats suggested by the mammals in the deposit.

Possibly other predators, such as *Dasyurus* or owls contributed to the bone sample, but Devil's Lair does not show an overwhelming preponderance of small (mouse or rat sized) mammals as do some other deposits (e.g. those described by Archer and Baynes 1972) interpreted as accumulated by owls or *Dasyurus.*

Our provisional belief is that the bone sample in the main represents the leavings of human beings, but that other predators may have contributed remains of their own prey or modified the human refuse.

Bias in the sample

The bone recovered from Devil's Lair is generally well preserved, yet there is marked imbalance in the frequency of occurrence of different parts of the skeleton within most species.

For example, we examined *Macropus fuliginosus* specimens from Trench 6, assembling all bones attributable to this species, not only those cranial and post cranial elements admitted to our faunal analysis, but also vertebrae, ribs and other elements not so admitted. There were large discrepancies between the numbers of bones and teeth of all kinds actually present and the numbers which would have been present if all teeth and bones of all *M. fuliginosus* individuals represented in our sample had been left lying within the confines of Trench 6. Discrepancies in numbers of teeth, of bones of the hands and feet, and of vertebrae, are set out in Table 1.

There appeared to be similarly large discrepancies between numbers actually present and expected numbers of long limb bones, pelvis, and so on for all parts of the skeleton, but because these were all fragmented, the discrepancies are not easily quantified and tabulated. For example in the "top" subdivision of brownish earthy layer, at least 7 individuals of *M. fuliginosus* were represented. But there were only 2 distal and no proximal fragments of humerus, only 1 fragment of radius, only 2 proximal and no distal fragments of femur and so on.

Perhaps the most striking discrepancy was in the distinctive large lower incisor teeth. Only 1 of these (73.8.977, from a young animal) was recovered from the whole 2.27 cubic metres of deposit excavated from Trench 6. Yet, as shown in Appendix 3 at least 17 individuals of *M. fuliginosus* must have contributed to the sample, and it is very likely that 24 or even more individuals actually contributed.

If most of the animals represented were taken into the cave as whole carcases, cooked and eaten on the spot, and the bones discarded, one would expect considerable lateral scattering of the bones of any individual. But if most parts of the cave were used, there should be considerable overlap of the discarded scattered bones of several individuals of any of the more common species on any occupation floor. In an excavation sampling these old occupation floors, one would expect mixtures of individuals to be represented, but if distribution were random any particular anatomical element, such as the first lumbar vertebra, would be about as well represented as any other element, such as the fourth metatarsal of the right foot.

Our examination of *M. fuliginosus* from Trench 6 suggests that one or more selective processes have operated.

Many writers, especially under the stimulus of the "osteodontokeratic" concept of Dart (1957), have discussed such selective processes. Butchering of large carcases at the kill site followed by removal of some but not all the bones back to the campsite in dismembered joints (including the "schlepp effect") is often cited as biassing

Table 1

Macropus fuliginosus *in Trench* 6

Stratigraphic subdivision	Minimum number of individuals (juveniles in brackets)	Tooth most abundantly represented, and number present	Teeth		Bones of hand and foot		Vertebrae	
			Total present	Expected number	Total present	Expected number	Total present	Expected number
Dark earthy layer	1 (?)	0	0	20	0	104	0	50
Pale band	1 (?)	0	0	20	1	104	0	50
Flecked....lens	1 (1)	0	0	24	2	104	1	50
Second dark earthy layer....	2 (1)	2 x RI²	10	44	1	208	0	100
Cave pearl and bone layer....	2 (1)	(1 each of several)	8	44	7	208	4	100
Top, brownish earthy layer	7 (5)	7 x LI¹	30	160	26	728	15	350
Upper middle, brownish earthy layer	2 (1)	2 x LI¹	7	44	1	208	3	100
Lower middle, brownish earthy layer	8 (6)	7 x LI¹	43	184	107	832	52	400
Bottom, brownish earthy layer	2 (2)	2 x RI¹	8	48	20	208	11	100

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bone samples, for example by White (1952, 1953a, b, 1955), Innskeep and Hendy (1966), Perkins and Daly (1968), Daly (1969), or Perkins (1969), Dart (1954, 1957), Kitching (1963), Wolberg (1970), and others have stressed selection of some bones for use as tools. Brain (1967a, b, c, 1970), Isaac (1967), Schaller and Lowther (1969) and others stress carnivores acting alone, or carnivores acting on accumulations of bone left by human beings. White (1953c, 1956) describes personal or group habits and customs biassing bone samples.

In the case of Devil's Lair it seems unlikely that the discrepancy between bones present and bones expected has anything to do with off site butchering methods because most of the animals eaten were small and even a large kangaroo carcase can be carried by a man. But selection of bones for making tools can be inferred. For example it seems likely that the dearth of kangaroo lower incisors, mentioned above, was due to the removal of these teeth, or even of whole jaws containing them, for use as tools. Dortch and Merrilees (1972) illustrate a wallaby lower incisor with transverse incisions which may have been used to bind it to a stick, or may have resulted from such binding. Kangaroo lower incisors may well have been used similarly. The one kangaroo lower incisor found in Trench 6 had a very open root, such as one finds in very young animals, and hence may have been too fragile to serve as a tool. Other bone implements from the deposit are described by Dortch and Merrilees (1973) and Dortch (1974).

It is probable also that much bone was eaten by man or by devils and reduced to fragments small enough to pass through our screens. Douglas, Kendrick and Merrilees (1966) report observations on living devils and their effects upon bone, and the specimens concerned, still preserved in the Western Australian Museum, include a good deal of finely comminuted bone recovered from the faeces of the devils observed. Not only devils, but also human beings accustomed to using their teeth more vigorously than do most modern people, might fragment and ingest appreciable quantities of bone.

Many of the bone fragments in our sample show rounding and smoothing of what initially must have been jagged fracture edges. Many tooth bearing fragments (e.g. *Bettongia penicillata* specimens 73.8.719, 73.9.51, 73.12.379) show this rounding, and also many small fragments of post cranial bones of many kinds. At present we are uncertain about the smoothing process involved. It might be from human handling and use, for example to flesh animal skins or smooth wooden spear shafts. It might be from the trampling of fragments into a sandy floor, as described by Brain (1967b, c), or from passage through and corrosion in the gut of devils or human beings. Whatever the rounding process, it is reasonable to suggest it converts some proportion of the original bone sample into particles below the limit of our recovery methods.

The bone sample as an index of human use of the cave.

By assuming that all the bone recovered in our excavations came from animals eaten in the cave by humans, and by making the other assumptions set out below about the bone sample, we arrive at a very rough estimate of the extent to which the cave might have been used from about 19 000 yr B.P. to about 12 000 yr B.P. To do this, we have combined data from first orange brown earthy layer in Trench 5 and brownish earthy layer in Trench 6.

For the purpose of comparing estimates of minimum numbers of individuals of a particular species in one stratigraphic unit with the same species in another, we have made no attempt to correct any overestimation shown in the Appendix 1 tables. However, for the purpose of interpreting our bone sample in terms of the meat it represented, we must compare estimates for different species, and therefore have applied correction factors to the numbers obtained from the appendix tables. These correction factors are based on our study of the degree of overestimation in *Sminthopsis, Pseudocheirus* and *Macropus fuliginosus* reported in Appendix 3. We multiply the numbers shown in the appendix tables for *Macropus fuliginosus*, the only large animal present by $\frac{1}{2}$, and for the animals of intermediate body size (*Dasyurus, Sarcophilus, Thylacinus, Isoodon, Perameles, Trichosurus, Pseudocheirus, Potorous*, both species of *Bettongia, Petrogale, Macropus eugenii, M. irma* and *Setonix*) by $\frac{2}{3}$. We leave unchanged the numbers shown for all other vertebrate taxa which are of small size. Thus corrected, the numbers of individuals for first orange brown earthy layer in Trench 5 and brownish earthy layer in Trench 6 together are:

large kangaroos	27
animals of intermediate size	653
small vertebrate animals	566

To translate these findings into numbers of human meals, we assume that about 1 kg live weight of any animal would constitute one meal of meat for one person (cf. McArthur in Mountford 1960; Gould 1967). Each large kangaroo might then represent 20 meals, each animal of intermediate size 2 meals, while 5 small animals might be required for one meal. On these assumptions, at least 2 000 meals of meat are represented by the bone sample under consideration. It is unlikely that the human occupants of the cave lived entirely on vertebrate prey animals. If we assume that half their diet was plant food, remains of which have dissipated or have not been recognised in our excavations, and invertebrate animals, then at least 4 000 meals are represented by our bone sample.

The area excavated in Trenches 5 and 6 is probably not more than 1% of the area of cave floor below which a thick deposit might exist. If we assume that the 19 000 to 12 000 yr B.P. section of the deposit is typified in Trenches 5 and 6, then the bone sample from these trenches represents only about 1% of what could be re-

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covered from the cave. Thus at least $4\,000 \times 100 = 400\,000$ meals were eaten in the cave over a period of about 7 000 years. This is an average of about 60 meals per year.

A family group of 5 people spending 6 consecutive days in the cave and eating 2 meals (one of meat) each day in the cave would account for 60 meals. Thus one visit to the cave each year by such a family group would be enough to account for the minimum number of individual prey animals represented by our bone sample.

However it is likely that our estimates of minimum numbers of individuals greatly under-estimate the actual number of animals eaten in the cave (cf. Perkins in Matolcsi 1973). Also the tables of Appendix 1 suggest that the rate of occupancy of the cave was far from uniform. It is reasonable to suggest alternatives to this concept of a small family group staying in the cave for a few days at a time once a year. Such a group might have stayed there for longer periods less often and the digging and presumably use of the large Pit 2 (described by Dortch and Merrilees 1973) reinforces this suggestion. Or the cave may have served as a meeting place for a larger number of people for a few days even less often.

At present we are unable to choose between these or other possible alternatives. Indeed, there are so many unexamined and in some cases un-examinable assumptions underlying our calculations that we conclude merely that our sample indicates intermittent rather than continuous human occupation of the cave between 19 000 and 12 000 years ago.

The fossil mammal fauna of Devil's Lair

We have recognised 35 species of mammals among material recovered from the 1970, 1972 and 1973 excavations in Devil's Lair, and these are listed in Table 2. Descriptions of the animals concerned, together with vernacular names, authors of systematic names, and a selected list of scientific studies are given by Ride (1970).

Table 2

Mammal species recorded from the 1970, 1972 and 1973 excavations in Devil's Lair

Carnivorous marsupials
> *Dasyurus geoffroii*
> *Phascogale tapoatafa*
> *Antechinus flavipes*
> *Sminthopsis murina*
> *Sarcophilus harrisii*
> *Thylacinus cynocephalus*

Bandicoots
> *Isoodon obesulus*
> *Perameles*—species not so far identified

Possums
> *Trichosurus vulpecula*
> *Pseudocheirus peregrinus*
> *Cercartetus concinnus*

Rat-kangaroos
> *Potorous tridactylus*
> *Bettongia penicillata*
> *Bettongia lesueur*

Wallabies and kangaroos
> *Petrogale*—species not so far identified
> *Lagorchestes*—species not so far identified
> *Macropus eugenii*
> *Macropus irma*
> *Macropus fuliginosus*
> *Setonix brachyurus*

Native rats and mice
> *Hydromys chrysogaster*
> *Pseudomys albocinereus*
> *Pseudomys occidentalis*
> *Pseudomys shortridgei*
> *Pseudomys praeconis*
> *Notomys*—species not so far identified
> *Rattus* (probably all *R. fuscipes*)

Bats
> *Macroderma gigas*
> *Nyctophilus timoriensis*
> *Nyctophilus geoffroyi*
> *Eptesicus pumilus*
> *Chalinolobus gouldii*
> *Chalinolobus morio*
> *Pipistrellus tasmaniensis*
> *Tadarida australis*

Our estimates of minimum numbers of each mammal species from the 1972 and 1973 excavations, and also of other vertebrate taxa, arranged stratigraphically, are tabulated in Appendix 1. Dortch and Merrilees (1972) similarly tabulate such estimates for the 1970 excavation.

Some species are represented by a few individuals only, others by many individuals. We have attempted to show in Figures 4 and 5 the changes in relative proportions of the species more abundantly represented from about 19 000 to about 12 000 years ago in the 1972 and 1973 excavations. Our sample from about 25 000 to about 19 000 years ago, as shown in Appendix 1, is so small that we have not attempted to show relative proportions of the various species involved.

The modern mammal fauna of the Devil's Lair district

As with most other localities in Australia, the mammal fauna now living in the Devil's Lair district is not the same as that present just before the arrival of European man. Drastic changes to habitats, efforts to exterminate native "pests", and introduction of exotic species have all had profound effects on the mammal populations. Therefore we use the term "modern mammal fauna" to mean that occurring in immediately pre-European times. This fauna is the only one meaningful for comparison with the fossil fauna, since it represents the end product of the prehistory of the area.

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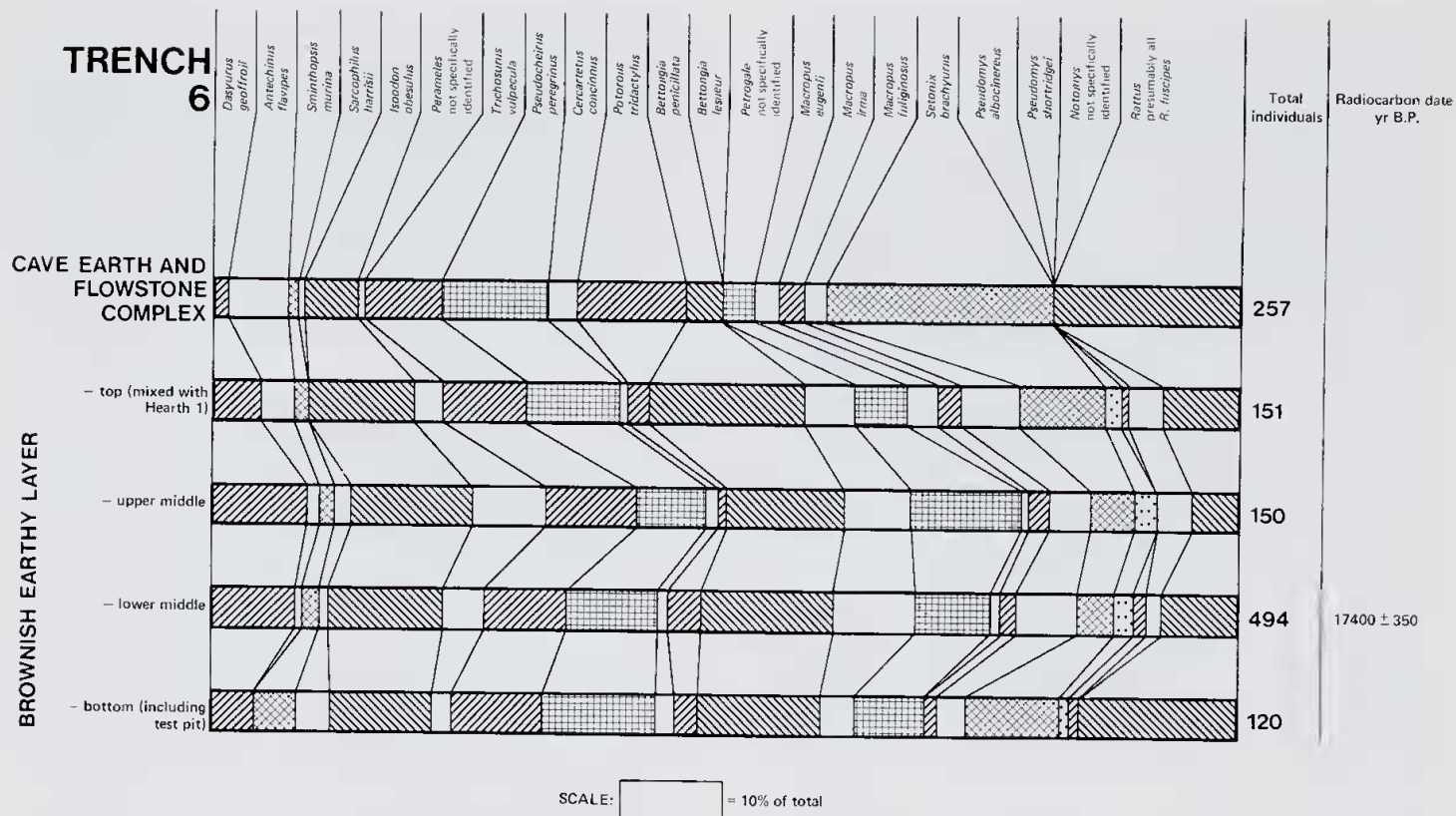
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Figure 4.—Relative proportions of the well represented mammal species in two major stratigraphic divisions in Trench 6, Devil's Lair.

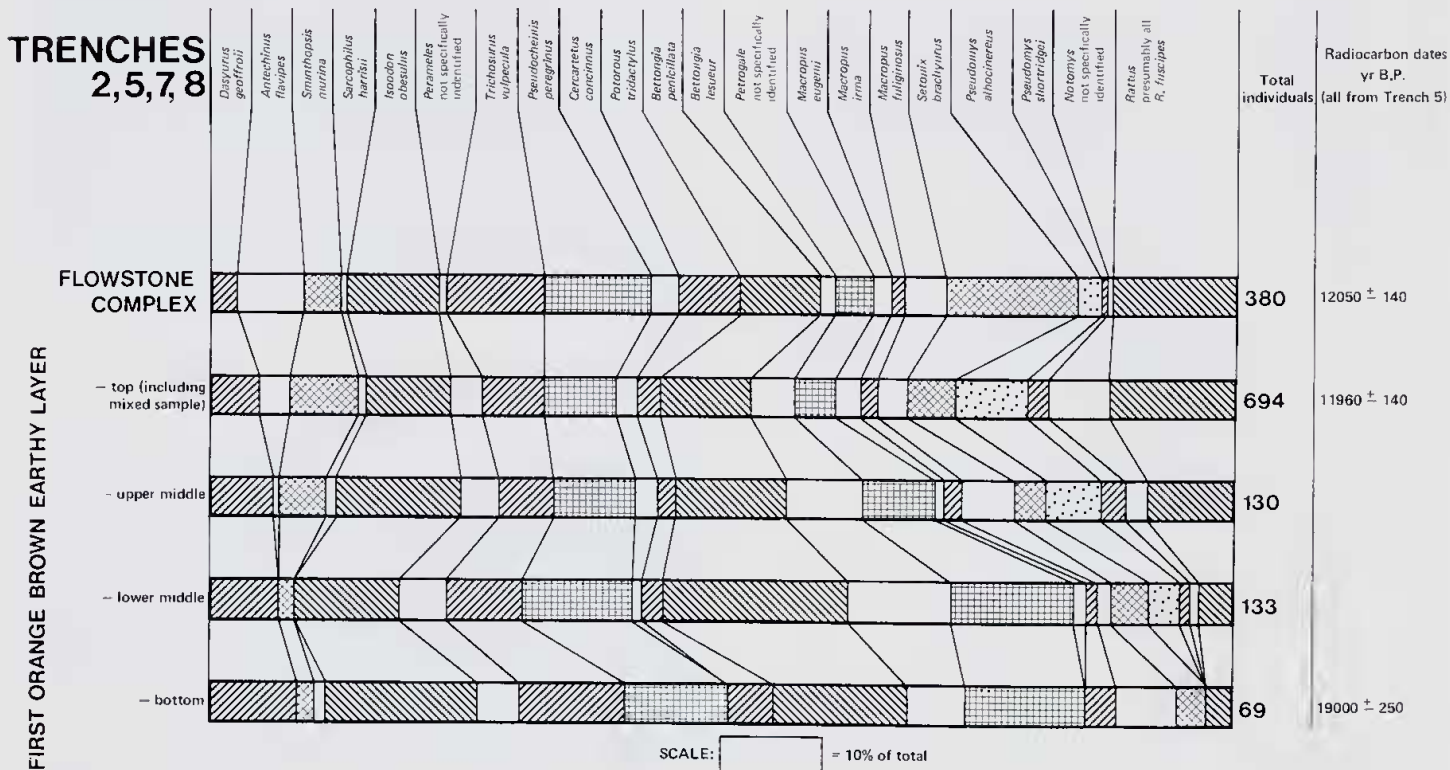

Figure 5.—Relative proportions of the well represented mammal species in two major stratigraphic divisions in Trenches 2, 5 7 and 8 combined, Devil's Lair.

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Appendix 2 gives details of museum and other records forming the basis of our reconstruction of the modern mammal fauna of the Devil's Lair district. These enable us to refine previous attempts (e.g., Merrilees 1968, Archer and Baynes 1972). We have taken into account the likely ranges from Devil's Lair covered by predators bringing prey back to the cave; and by "Devil's Lair district" we mean this predator determined area.

Table 3

Mammal species we are confident were present in the modern fauna of the Devil's Lair district

Carnivorous marsupials

    Dasyurus geoffroii
    Phascogale tapoataja
    Sminthopsis murina

Possums

    Tarsipes spencerae
    Trichosurus vulpecula
    Pseudocheirus peregrinus
    Cercartetus concinnus

Rat-kangaroos

    Bettongia penicillata

Wallabies and kangaroos

    Macropus fuliginosus
    Setonix brachyurus

Native rats and mice

    Hydromys chrysogaster
    Rattus fuscipes

Table 4

Mammal species probably in the modern fauna of the Devil's Lair district

Carnivorous marsupials
    Antechinus flavipes

Bandicoots
    Isoodon obesulus

Rat-kangaroos
    Potorous tridactylus

Wallabies and kangaroos
    Macropus irma

Native rats and mice
    Pseudomys shortridgei
    Pseudomys praeconis
    Rattus tunneyi

Bats
    Nyctophilus timoriensis
    Nyctophilus geoffroyi
    Eptesicus pumilus
    Chalinolobus morio
    Pipistrellus tasmaniensis

Carnivorous eutherians
    Canis familiaris

Table 5

Mammal species possibly forming part of the modern fauna of the Devil's Lair district

Wallabies and kangaroos
    Macropus eugenii
Bats
    Chalinolobus gouldii
    Tadarida australis

We are confident that the species listed in Table 3 were part of the modern fauna, and we think it probable that the species listed in Table 4 were too. Table 5 lists mammals recorded within 75 km of Devil's Lair in modern time, but whose inclusion in the modern fauna of the Devil's Lair district is doubtful for reasons discussed in Appendix 2.

Comparison of modern and fossil mammal faunas from Devil's Lair

By combining the species listed in Tables 3 and 4, we suggest that the mammal fauna of the district just before it was affected by European man probably included 25 species, and it may have included the 3 additional species listed in Table 5. Of this total of 28 species, only *Tarsipes spencerae*, *Rattus tunneyi* and *Canis familiaris* are not so far recorded in the fossil fauna from Devil's Lair.

The fossil fauna listed in Appendix 1 includes 33 species, and 2 additional species were recovered from the 1970 excavation, namely *Lagorchestes* sp. and *Chalinolobus morio*, discussed below. Of these 35 fossil species (see Table 2), the 10 species listed in Table 6 appear not to have formed part of the modern fauna of the Devil's Lair district.

Small, frail remains of *Tarsipes spencerae* may have escaped detection. Although the species is known to live at present in heaths in many localities between Yanchep and Dongara, only one fossil specimen (Archer 1973) has been recognized from any of the numerous caves in this region, many of them containing large accumulations of bone from owl pellet deposits. But we suggest that the absence of *Rattus tunneyi* and *Canis familiaris* from the fossil fauna so far recognized represents a real absence of these two species from the Devil's Lair district in ancient times.

Dortch and Merrilees (1972) suggested that a single canine tooth (70.12.202) found by them in 1970 might have represented a Dingo, but this tooth has been examined subsequently by Professor N. W. G. Macintosh and colleagues, and is considered by them (Macintosh, personal communication) in fact to represent *Sarcophilus*. No specimen representing *Canis* was found in the 1972 and 1973 excavations. However, the carnivorous marsupial of size comparable with *Canis* namely *Thylacinus*, is represented only by two isolated teeth. The possibility remains that both the marsupial and the

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eutherian carnivores were present, but were diffi-
cult to catch or distasteful to eat, and there-
fore are not well represented, or not repre-
sented at all, in the litter left lying in the
cave. However, the Dingo is generally believed
to have been introduced into Australia by Abo-
rigines migrating in Recent time (Jones 1970),
and our evidence is consistent with this view.

Archer and Baynes (1972) postulate that *Rat-
tus tunneyi* extended its range along the west-
ern coastal plain into the extreme south west of
Western Australia, including Devil's Lair dis-
trict, only in Recent time. This is supported
by unpublished studies by one of us (J.K.P.) of
a stratified deposit in a cave near Augusta, in
which *Rattus tunneyi* occurs only in the top
layers of the deposit, dated on charcoal as 2900
± 80 radiocarbon years B.P. (date SUA-227)
or later.

Dortch and Merrilees (1972) report the pres-
ence of a single specimen (70.12.1132) tenta-
tively ascribed to *Lagorchestes* sp. Unless the
specimen is aberrant, we concur in this identi-
fication. Among the specimens simply listed
as "bats" by Dortch and Merrilees (1972), we
have recognized three as *Chalinolobus morio*.
The three specimens (70.12.776, 70.12.911 and
71.1.223) come from three different levels in
Trench A1. Neither *Lagorchestes* sp. nor *Chali-
nolobus morio* was recognized in the material
excavated in 1972 and 1973.

Even though some species of mammals pres-
ent as fossils were not present in the modern
fauna of the Devil's Lair district, all are pres-
ent in the modern fauna of Australia as a whole
(including Tasmania), and only two of these
species seem to have disappeared from the Aus-
tralian mainland. These are *Thylacinus cyno-
cephalus* and *Sarcophilus harrisii*, both of which
are known to have survived on the mainland
until late Recent time (Partridge 1967, Archer
and Baynes 1972).

Table 6

*Mammal species not forming part of the modern fauna
of the Devil's Lair district, but recorded from the 1970,
1972 and 1973 excavations in Devil's Lair*

Carnivorous marsupials
   Sarcophilus harrisii
   Thylacinus cynocephalus

Bandicoots
   Perameles sp.

Rat-kangaroos
   Bettongia lesueur

Wallabies and kangaroos
   Petrogale sp.
   Lagorchestes sp.

Native rats and mice
   Pseudomys albocinereus
   Pseudomys occidentalis
   Notomys sp.

Bats
   Macroderma gigas

Thus it seems that 2 or possibly 3 mammal
species have arrived in the Devil's Lair district,
and at least 10 species have disappeared (see
Table 6) since the fossiliferous parts of the de-
posit were sealed by thick flowstone about 12 000
years ago.

Modern distribution patterns and habitat adaptations of mammal species

On the basis of general patterns revealed by
unpublished studies of modern mammal distri-
butions in south western Australia made by
one of us (A.B.), we have divided the species
listed in Table 2 into two categories. These are
"forest mammals" and "non-forest mammals".
The forest mammals, listed in Table 7, are de-
fined as those species whose modern distribu-
tions include the "forest block", which is the
area mapped by Gardner (1944, Plate X) as
sclerophyllous forest and mesophytic forest. It
includes the formations mapped by Smith (1973)
in the Busselton-Augusta region as high open
forest and open forest. *Sarcophilus harrisii*
and *Thylacinus cynocephalus* are regarded as
forest mammals on the basis of their modern
Tasmanian distributions, even though they ap-
parently did not persist in Western Australia
into modern times. The non-forest mammals,
listed in Table 8, are defined as those species
recorded from Devil's Lair whose distributions
do not include the forest block. The distri-
bution studies suggest that the natural eastern
margin of the forest block, where it merged
into woodland or shrub formations (before most
of the area was cleared for agriculture), repre-
sents an important demarcation of modern
faunas. The ranges of most forest mammals
extended beyond this line, but it appears to
have represented a barrier to non-forest mam-
mals in immediately pre-European times.

No thorough investigation has been made of
differences between the mammal faunas of the
Karri high open forest and the Jarrah-Marri
open forest. It is possible that fewer mammal
species occur naturally in the Karri forest, but
in the absence of data we assume that all the
forest mammals occurred in both.

Species which are restricted in range of dis-
tribution or habitat are the most useful indi-
cators of environmental conditions. The forest
mammal with the most restricted distribution is
Potorous tridactylus. In Western Australia,
where it may now be extinct, *P. tridactylus* ap-
pears to have been limited to the area of the
extreme south west in which some rainfall oc-
curs throughout the summer. There it prob-
ably inhabited densely vegetated watercourses
and wet heaths. *Setonix brachyurus* also finds
densely vegetated forest gullies an optimum
habitat; but it has a wider distributional range,
from Gingin Brook in the north (Roe 1971) to
the Hunter River east of Bremer Bay. The
latter locality represents an eastward extension
of the previously known range. It is based
upon a dentary (M10519), considered to repre-
sent a modern animal, which was picked up in
1970 by W. H. Butler. The distribution of

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Setonix brachyurus within the northern part of the forest block appears to have been restricted to the western areas; its range probably did not reach the eastern margin.

The distribution of *Rattus fuscipes* in Western Australia is unlike that of any other mammal. It occurs in the southern part of the forest block, principally along river systems, and also in coastal dune systems and heaths from Jurien Bay round to Israelite Bay. There appears to be no reliable evidence for its occurrence in the northern areas of the forest block. Both of the specimens from that area cited by Taylor and Horner (1973), Western Australian Museum M5815 and C.S.I.R.O. CM859, have been examined by one of us (A.B.) and are considered to be *Rattus rattus*. Near Devil's Lair *Rattus fuscipes* has been collected live both in regenerating Peppermint open scrub and Karri high open forest.

It is possible that the ranges of the three forest mammals *Macropus eugenii*, *Chalinolobus gouldii*, and *Tadarida australis*, listed in Table 3, did not cover the extreme south west of the forest block. In addition little is known of the habitat requirements or full ranges of the other bat species included in Table 7. Some uncertainty also exists in the cases of *Sarcophilus harrisii* and *Thylacinus cynocephalus*.

Table 7

Forest mammals recorded from the Devil's Lair deposit

Carnivorous marsupials
  Dasyurus geoffroii
  Phascogale tapoataja
  Antechinus flavipes
  Sminthopsis murina
  Sarcophilus harrisii
  Thylacinus cynocephalus

Bandicoots
  Isoodon obesulus

Possums
  Trichosurus vulpecula
  Pseudocheirus peregrinus
  Cercartetus concinnus

Rat-kangaroos
  Potorous tridactylus
  Bettongia penicillata

Wallabies and kangaroos
  Macropus eugenii
  M. irma
  M. fuliginosus
  Setonix brachyurus

Native rats and mice
  Hydromys chrysogaster
  Rattus fuscipes

Bats
  Nyctophilus timoriensis
  N. geoffroyi
  Eptesicus pumilus
  Chalinolobus gouldii
  C. morio
  Pipistrellus tasmaniensis
  Tadarida australis

*Well represented through the deposit and included in Figures 4 and 5.

Records indicate that the other 13 forest mammals, not discussed above, occurred right through the forest block. Of these *Phascogale tapoataja*, *Antechinus flavipes*, and *Pseudocheirus peregrinus* also occurred in the high rainfall woodlands. *Hydromys chrysogaster*, the Water Rat, is a specialized species normally only found in or adjacent to bodies of water. The remainder have been recorded from a broad spectrum of habitat types, and some range far into the dry inland of Australia: e.g., *Dasyurus geoffroii* and *Trichosurus vulpecula* both formerly occurred widely in desert areas.

Table 8

Non-forest mammals recorded from the Devil's Lair deposit

Bandicoots
  Perameles sp.

Rat-kangaroos
  Bettongia lesueur

Wallabies and kangaroos
  Petrogale sp.
  Lagorchestes sp.

Native rats and mice
  Pseudomys albocinereus
  P. *occidentalis*
  P. shortridgei
  P. *praeconis*
  Notomys sp.

Bats
  Macroderma gigas

* Well represented through the deposit and included in Figures 4 and 5.

Since we are unable to identify some of the non-forest mammals listed in Table 8 beyond generic level, we here discuss the species most likely on biogeographical grounds to be represented in Devil's Lair—*Perameles bougainville*, *Petrogale penicillata*, *Lagorchestes hirsutus* and *Notomys mitchellii*.

Six non-forest mammals share a common distributional characteristic, that is they have been recorded along the inland side of the forest block. These are *Perameles bougainville*, *Bettongia lesueur*, *Pseudomys albocinereus*, *P. occidentalis*, *P. shortridgei* and *Notomys mitchellii*. Of the other four species, *Petrogale penicillata* and *Lagorchestes hirsutus* are recorded from just north east of the forest block, *Macroderma gigas* from the coastal plain north west of the forest block, and *Pseudomys praeconis* from just north of the forest block. The modern distributions of all five species of native rats and mice, and possibly *Bettongia lesueur*, also included the northern part of the western coastal plain.

Although only two of the non-forest mammals (*P. shortridgei* and *P. praeconis*) extended south on this plain along the western side of the forest block in modern time, we suggest below that all

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our non-forest mammals occupied the southern part of the western coastal plain at some time during the accumulation of the Devil's Lair deposit.

The south western populations of *Petrogale*, restricted in modern time to rocky hills inland from the forest block, are probably conspecific with other populations occurring in arid localities such as the Macdonnell Ranges (Ride 1970), but we are not sure that any is conspecific with the Devil's Lair population. Most *Petrogale* species now seem to inhabit rock outcrops which shield them from extremes of temperature.

Macroderma gigas ranged over much of desert and tropical Western Australia (Douglas 1967), but its remains, presumably of Recent age, are widespread in caves between Yanchep and Dongara. In one deposit it was present throughout the Recent (unpublished data from Hastings Cave, A.B.) associated with a mammal fauna characteristic of heath habitats (Lundelius 1960, with the qualifications of Archer and Baynes 1972).

Sand appears to be a substrate requirement of *Pseudomys albocinereus* and most species of *Notomys*. While *P. albocinereus* occurs mainly in coastal sand plains carrying open heath, *Notomys mitchellii* occurs not only in such habitats but also on inland sand plains carrying open heath and other shrub formations. *Perameles bougainville* probably also occurred in sand plains in south western Australia (Ride 1970).

Although *Pseudomys occidentalis* remains are known from the surface in caves in the coastal sand plains, modern specimens have mainly been collected in areas which have a loam or gravelly sand substrate.

Insufficient information is available to determine the habitats occupied by *Bettongia lesueur*, *Largorchestes hirsutus*, *Pseudomys shortridgei* and *P. praeconis* in the south west of Australia.

Changes in the mammal fauna around Devil's Lair, and interpretation

We have attempted to quantify information on the mammals from our excavations, but have shown that the results must be viewed with caution. We have not applied statistical tests. In order to assess changes in the mammal fauna, we distinguish between the small sample available for the period 25 000 to 19 000 years ago and the larger sample available for the period 19 000 to 12 000 years ago, and between species which are represented only in small numbers widely spaced in the deposit, and those which are present at most levels (even if only in small numbers).

The relative abundances of the well represented species for the later period in Trench 6 and in the Trench 2, 5, 7 and 8 complex are shown as bar diagrams in Figures 4 and 5 respectively. The stratigraphic groupings shown in these figures seem to us broad enough to minimize stratigraphic uncertainties in our sampling procedures and to allow comparisons to be made between Trench 6 and Trenches 2, 5, 7 and 8.

We infer real changes in relative abundance where species show similar trends from level to level in Trench 6 and in Trenches 2, 5, 7 and 8. We make no such inferences where trends are dissimilar.

We have compared the change in relative abundance of each species from one stratigraphic level to the next higher level in Trench 6 with the corresponding change in Trenches 2, 5, 7 and 8. The numbers of species synchronously increasing, decreasing and changing in opposite ways are set out in Table 9. There is no case of a species remaining unchanged. Our comparisons were made using Figures 4 and 5.

The substantial proportion of species changing in opposite ways at all levels (right hand column of Table 9) suggests that much of the observed change is random. However, there appears to be some decrease in randomness towards the top of the deposit. This is explained by the trend shown in the central column of Table 9. More species decline in the upper levels of the deposit.

Figures 4 and 5 show that, between the top subdivision of brownish/first orange brown earthy layer and (cave earth and) flowstone complex, 5 non-forest mammals (*Perameles* sp., *Bettongia lesueur*, *Pseudomys albocinereus*, *P. shortridgei*, and *Notomys* sp.) and 4 forest mam-

Table 9

Numbers of species changing in relative abundance in the same way in Trench 6 and in Trenches 2, 5, 7 and 8 from stratigraphic level to next higher stratigraphic level—data of Figures 4 and 5, dealing with 21 species well represented through the deposit.

Stratigraphic level	No. of species increasing in relative abundance	No. of species decreasing in relative abundance	No. of species showing opposing trends, or changes in one trench but not in the other
(Cave earth and) flowstone complex			
Brownish/first orange brown earthy layer -top	5	9	7
-upper middle	5	6	10
-lower middle	7	5	9
-bottom	7	2	12

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mals (*Dasyurus geoffroii, Sminthopsis murina, Bettongia penicillata* and *Macropus eugenii*) decline. These forest mammals are all species recorded from a broad spectrum of habitats. At the same time, the 2 species (*Potorous tridactylus* and *Setonix brachyurus*) most restricted within forest show their greatest increase.

Of the 21 species shown in Figures 4 and 5, 15 species (* in Table 7) are forest and 6 species (* in Table 8) are non-forest mammals.

We next analyse the forest and non-forest mammals which change in relative abundance from level to level in the same way in Trench 6 as in Trenches 2, 5, 7 and 8. The results (in Table 10) suggest that these forest mammals show no discernible trend from about 19 000 years ago (the time of deposition of the bottom subdivision of brownish/first orange brown earthy layer) to about 12 000 years ago (the time of deposition of cave earth and flowstone complex). On the other hand, the non-forest mammals analysed at first increase and then decrease in relative abundance during this period.

We have no data from Devil's Lair on trends in relative abundance of mammal species between about 12 000 years ago and modern time, but we have shown above that 10 species (Table 6) which were present about 12 000 years ago were not present in modern time, whereas only 2 (or at most 3) species which were present in modern time were not present in the Devil's Lair deposit. This net impoverishment of the mammal fauna of the district is mainly of the non-forest mammal component. The disappearance of the 2 forest mammals (*Sarcophilus harrisii* and *Thylacinus cynocephalus*) may be causally related to the appearance of *Canis familiaris*.

Thus we suggest that most of the non-forest mammals began to decline in terminal Pleistocene time, that the decline was marked by about 12 000 years ago, and that it continued subsequently until at some time not at present known, these species became extinct locally. On the other hand, the forest mammals appear to have fluctuated in relative abundance, but to have persisted into modern time.

At present forest habitats predominate over non-forest habitats in the Devil's Lair district. As described in the Introduction, Devil's Lair is now surrounded by Karri forest which gives way within 2 km to the east to very extensive Jarrah-Marri forest, and within 2 km to the west to low tree and shrub formations. For our purposes we divide the vegation into a "forest zone" occupied by the forest mammals and a "non-forest zone" to which the non-forest mammals are restricted. Our forest zone comprises the Karri high open forest and Jarrah-Marri open forest mapped by Smith (1973). The main formation in our non-forest zone is Smith's Acacia open heath, but it includes small areas of Peppermint open scrub, Banksia open woodland, Peppermint low woodland, Jarrah low open forest, and Peppermint low open forest. The boundary between Karri high open forest (Figure 6) and Acacia open heath (Figure 7) is now very sharply demarcated near Devil's Lair by a crest which shelters the Karri forest from the prevailing winds. We include two low tree formations in our non-forest zone because the same plant communities at times pass from shrub formations to these low tree formations as they approach climax, and they probably continue to harbour non-forest mammals. This applies particularly to communities in which Peppermint is an important component. On the other hand, the high open and open forest which we include in our forest zone are tree formations from very early stages of their cycles.

The faunal changes described above suggest there was a diminution or contraction away from Devil's Lair of the non-forest zone which began to affect the fauna in terminal Pleistocene time and continued into the Recent. It is tempting to suggest climatic change as the main cause of this inferred vegetational change, but glaciceustatic rise in sea level must also be considered as a contributing or indeed even as the main cause.

There seems to have been a lag between maximum glaciation and maximum glacioeustatic fall in sea level, and the extent of both lag and fall have been variously estimated, even for the last glaciation (Milliman and Emery 1968, Guil-

Table 10

Comparison of numbers of species of forest with non-forest mammals which show the same trends in relative abundance in Trench 6 and Trenches 2, 5, 7 and 8 from one stratigraphic level to the next higher level—data from Figures 4 and 5.

Stratigraphic level	Species showing same trend in Trench 6 as in Trenches 2, 5, 7, 8. (see Table 9)	Forest mammals increasing in relative abundance	Forest mammals decreasing in relative abundance	Non-forest mammals increasing in relative abundance	Non-forest mammals decreasing in relative abundance
(Cave earth and) flowstone complex					
Brownish/first orange brown earthy layer -top	14	5	4	0	5
-upper middle	11	5	3	0	3
-lower middle	12	5	4	2	1
-bottom	9	2	2	5	0

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Figure 6.—Karri growing on the eastern side of the ridge, near Devil's Lair. The density has been reduced by felling.

sea level rose from 16 000 yr. B.P. to, say, 13 000 yr. B.P., the non-forest zone may have been narrowed, but may still have exceeded the hunting range of predators operating from Devil's Lair, so that the proportions of mammals obtained by them from different zones would remain unchanged.

Figure 7.—Acacia open heath on the seaward slope of the ridge west of Devil's Lair.

cher 1969, Jongsma 1970, Richards 1970, Mörner 1971, Gill 1971, Walcott 1972, Andrews 1973, Hopkins 1973 and many others). The subject is controversial and we here assume that at some time after 19 000 yr B.P. the sea west of Devil's Lair fell to 100 m or more below its present level, and then began to rise, reaching about 40 m below its present level by 12 000 yr B.P., and reaching its present level at some time in the Recent. We assume also that soundings in Hamelin Bay (Archdeacon 1878) reveal a topography which has not changed markedly since 19 000 yr B.P., whether submerged or not. On these assumptions, the sea coast would have lain more than 20 km west of its present position soon after 19 000 yr B.P., and more than 6 km west about 12 000 yr B.P., but has been close to its present position for several thousand years.

The boundary between forest and non-forest zones may have occupied more or less its present position near Devil's Lair at the time of lowest sea level, perhaps 16 000 years ago. This would have resulted in a non-forest zone some 30 km wide between it and the coast rather than the 3 km of the present day.

In this case, human hunters or other predators operating from Devil's Lair within a radius of about 10 km and hunting mammals impartially in forest and non-forest zones would have obtained forest and non-forest mammals in comparable proportions about 16 000 years ago. As

But by about 12 000 yr. B.P. the encroaching sea may have reduced the non-forest zone to less than 10 km width. Then the Devil's Lair hunters would have brought back to the cave a smaller proportion of non-forest than of forest mammals. Subsequently with continued encroachment of the sea, the proportion of non-forest mammals would have fallen further. On this view, the critical time at which the extent of the non-forest zone available to hunters fell below their hunting range would have coincided with the end of accumulation of first orange brown earthy layer in Trench 5, for example. By the time that flowstone complex accumulated, forest mammals would have formed a larger proportion of the hunters' prey. This may have been a time of very rapid rise in sea level (Cullen 1967).

Such a view fits our data, but it may seem unlikely that the boundary between forest and non-forest zones would have been stable. This boundary probably results from dynamic balance of a number of determinants such as amount and distribution of rainfall, windiness, etc., which would have been subject to considerable fluctuation between 19 000 and 12 000 years ago. Churchill (1968) in his study of Karri, Jarrah and Marri extending back over much of Recent time has shown that rainfall characteristics rather than temperature determine the distribution of these species. Another determinant (Smith 1973), probably not subject to fluctuation, is topographic—shelter from the prevailing winds.

By analogy with other parts of the world, it would appear likely that temperature, quantity of rainfall, distribution of rainfall, windiness, evaporation rates and other climatic determi-

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nants of plant growth varied from 19 000 to 12 000 years ago, even for a middle latitude site with strong maritime influence like Devil's Lair. From consideration of the studies of Van Andel, Heath, Moore and McGeary 1967, Galloway 1967, Damuth and Fairbridge 1970, Howard and Hope 1970, Derbyshire 1971, Adam 1971, Bowler and Hamada 1971, Quinn 1971, Bowler, Thorne and Polach 1972, Colinvaux 1972, Costin 1972, Klein 1972, Löffler 1972, Mercer 1972, Van der Hammen 1972, Webster and Streten in Walker 1972, Bonatti and Gartner 1973, Goudie, Allchin and Hegde 1973, Kershaw 1973, Martin 1973, Van Geel and Van der Hammen 1973, and others, we suggest that temperature and quantity of rainfall may have increased, windiness decreased, and evaporation rates changed little from about 19 000 to about 12 000 years ago in the Devil's Lair district. In such circumstances, the forest boundary might have lain more or less in its present position, and our model outlined above (of human or other hunters based on Devil's Lair finding the proportion of non-forest zone available to the decreasing relative to forest) might be tenable.

The model above requires postulation of minimum environmental difference between late Pleistocene and present day conditions around Devil's Lair. But our data are also consistent with more substantial differences. For example it is possible that there was no Karri and all the forest mammals lived in open forests, or even that the non-forest zone surrounded Devil's Lair.

However, we are able to suggest that a forest barrier separated Devil's Lair from the wide variety of vegetation formations on the inland side of the forest block. While our forest mammals include all the species recorded in modern time from the forest block, except *Myrmecobius fasciatus* and *Tachyglossus aculeatus*, our non-forest mammals appear to be a biassed sample. There are about 46 species of mammals recorded from habitats near the forest block. Of these, 22 species inhabit both forest and non-forest habitats and are included in our "forest mammals". Of the remaining 24 species, only 10 are recorded from Devil's Lair and hence included in our "non-forest mammals".

We suggest that this reflects the types of habitats through which our non-forest mammal species had to pass to invade the Devil's Lair district. There appears to be a predominance of species characteristic of open heath habitats in our non-forest mammals. Such a bias would be consistent with species spreading south along a wider western coastal plain carrying predominantly shrub formations, round persistent forest acting as a barrier to inland populations.

Our sparse data on poorly represented species, and on the fauna of the period 25 000 to 19 000 years ago do not permit us to make many inferences. The minimum number of vertebrate individuals available to represent the period from about 25 000 to about 19 000 years ago is only 217 and the number of mammal species included is 21. (See Appendix 1 tables for

Trench 2 and the lowest part of Trench 5.) These 21 species represent both forest and non-forest zones, and we can infer therefore that both zones lay within reach of hunters based on Devil's Lair. Hence they could procure the same kinds of mammal prey as their successors, but it remains to be seen whether the proportions differed greatly.

Two *Pseudomys occidentalis* individuals were recovered from this small sample from the lowest levels in our excavations, whereas only a single tooth represents this species in the upper levels. This tooth, although it was found in Trench 6, could have come from old material dug out of Pit 2 in ancient times and distributed about what was then the cave floor. *P. occidentalis* may have disappeared early from the Devil's Lair district. However, little should be inferred from absence of any of the sparsely represented species. Archer and Baynes (1972) commented on the presence of *Hydromys chrysogaster* and *Nyctophilus timoriensis* in their deposit at Turner Brook (south of Devil's Lair) and the absence of these two species from the 1970 and previous excavations in Devil's Lair. They suggested that these two species might be found as excavation proceeded in Devil's Lair, and so it has proved. The virtual absence of *Pseudomys occidentalis* from the abundant remains so far recovered from upper levels in the Devil's Lair deposit may be just such another sampling accident.

Bats are only sparsely present in the Devil's Lair deposit. None occasions any surprise with the exception of *Macroderma gigas*, previously recorded by Cook (1960) and now confirmed by us. Douglas (1967) discusses possible reasons for major contraction in the former range of *M. gigas*, among them that it might find difficulty in exploiting even abundant prey in a forested area. Its presence in Devil's Lair may provide further evidence of a more extensive non-forest zone than now, or the few animals represented might be storm blown vagrants which sheltered in the cave but perished from cold or hunger without establishing a viable local colony.

Between the time of sealing with thick flowstone of the richly fossiliferous parts of the Devil's Lair deposit and modern time, various non-forest mammals disappeared. We have at present little understanding of the reasons for these disappearances, and little knowledge of their timing. Perhaps it is a simple matter of further shrinkage of the non-forest zone and expansion of the forest zone in Recent time as sea level continued to rise and/or annual or summer rainfall increased.

It is possible that non-forest mammals might have been able to maintain viable populations in the Devil's Lair district while a broad coastal corridor permitted contact with the main populations further north. When this link became attenuated as the corridor contracted towards its present dimensions, they may have been broken into isolated colonies which dwindled and eventually disappeared. The late arrival of *Rattus tunneyi* (see above) by a narrow coastal corridor may not be inconsistent with

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this concept. *R. tunneyi* is probably preadapted to success in this situation because it can maintain large populations in pockets of vegetation among mobile sand dunes at beach edges (e.g. specimens M8750-60 collected in 1970 at False Entrance, Shark Bay, by A.B.).

Conclusions

Our scanty data on the period 25 000 to 19 000 years ago, and our fuller data on the period 19 000 to 12 000 years ago, suggest that the mammal fauna in the Devil's Lair district remained approximately stable in the sense of neither gaining nor losing many species. Despite the growth of glaciers and ice sheets to a maximum and their subsequent decline in higher latitudes than that of Devil's Lair, despite any causative or consequent changes in climate on a world wide scale which might have had repercussions at Devil's Lair, and despite the corresponding changes in sea level, a sufficient variety of habitats was present to support a more diverse mammal fauna than that present just before the arrival of European man. A similar degree of stability is reported by Flood (1973) for an inland site in eastern Victoria from before 18 000 to about 8 000 years ago. In the case of our coastal site, stability may have begun to break down about 12 000 years ago.

Within this framework of late Pleistocene stability in species composition of the mammal fauna around Devil's Lair, fluctuations in relative proportions of the species probably occurred. Our stratigraphic control, understanding of the processes by which the deposit accumulated, and framework of radiometric dates are not yet sufficiently precise to define such fluctuations in detail. However our data do suggest a decline in mammals not known to inhabit forest. This trend appears to have been well established about 12 000 years ago and may have continued into the Recent. At all events, most of this group of mammals were locally extinct before European man arrived.

To account for the changes we have observed it is not necessary to postulate any major difference between the observable present and inferred past vegetational boundaries near Devil's Lair, and hence any marked climatic difference between late Pleistocene and modern time. But equally our data are consistent with climatic changes of some kinds, such as increase in total rainfall or in summer rainfall, in which case our findings would match in trend those reviewed by Fairbridge (1972). We are unable at present to separate climatic and non-climatic effects. As Calaby (in Mulvaney and Golson 1971), Freeman (1973) and others have pointed out, it is not easy to make palaeoenvironmental inferences from mammal remains. Lower vertebrates, land snails, pollen or other biota more stringently controlled by climate may be more useful. Our climatic model is based on analogy with distant regions and like other such models may be misleading (Ver-

stappen 1970, Galloway in Mulvaney and Golson 1971). All we can claim is that our climatic and sea level model is consistent with our data.

The first lists of mammal species present in the Devil's Lair deposit (Lundelius 1960, 1966; Cook 1960) were improved and extended by Dortch and Merrilees (1972), and we have been able to add to the list, perhaps most notably by the inclusion of *Pseudomys occidentalis*. Despite these additions to the faunal list from Devil's Lair, there are some notable absences: *Canis familiaris* on one hand, and species of *Sthenurus, Protemnodon*, and other large extinct marsupials on the other. We suggest that the Dingo did not arrive in the district until after flowstones sealed the richly fossiliferous deposit about 12 000 years ago, and perhaps *Sthenurus, Protemnodon* and other such taxa had become locally extinct before 25 000 years ago.

Since we know that a considerable depth of deposit remains to be excavated, we think it possible that these extinct taxa may yet be found. If the assessment of Jones (1973) is sound and there was a major episode of extinction "a geologically short time before 30 000 B.P.", this possibility seems more likely. On the other hand, if Aboriginal occupation of south western Australia is an ancient one, and if the arrival of the Aborigines is causally related to the extinction of *Sthenurus, Protemnodon* and the like (Merrilees 1968, 1973), then Jones' "geologically short time" might be tens or even hundreds of thousands of years. It remains to be seen whether the Devil's Lair deposit is deep enough to contain such extinct taxa.

We suggest that human occupation of the cave was sporadic and, if groups larger than single families were involved, very infrequent. Peterson (in Mulvaney and Golson 1971), Taylor 1972, and others have commented on the archaeological consequences of such situations, and in the case of Devil's Lair, with its low average rate of sedimentation, we cannot expect often to find the record of a single visit by a family group, which usually is "below the threshold of archaeological visibility". We may have to be content with the mixed traces of several or many visits unless we can refine our stratigraphic understanding very greatly. Thus it may be difficult to detect any seasonal rhythm in the use of the cave unless this was very regular and of long standing, and it may be difficult even to fit Devil's Lair into any such pattern as that mentioned by Wright (1971—following Hale and Flannery); we have as yet made no attempt to examine our data from these points of view.

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TRENCH 6

Stratigraphic divisions and subdivisions with radiocarbon date – yr B.P.	Depth below cave datum in line of section NW corner of trench, cm	Dasyurus geoffroii	Phascogale tapoatafa	Antechinus flavipes	Sminthopsis murina	Sarcophilus harrisii	Thylacinus cynocephalus	Isoodon obesulus	Perameles not specifically identified	Trichosurus vulpecula	Pseudocheirus peregrinus	Cercartetus concinnus	Potorous tridactylus	Bettongia penicillata	Bettongia lesueur
Floor of cave	54														
First dark earthy layer (Levels 1,2)	54- 77							1					1		
Cave earth and flawstone complex – Pale band (Level 3)	77- 87			1						1	2	2	1	1	
– Flecked lens (Levels 4,5)	87-c. 97	1+1?		4				3	1	4	2	2	3	3	1?
– Mixture including parts of subdivisions above and below				2				1		2	2	1	1		
– Second dark earthy layer (Level 6)	97-c.107	1		1				6		8	9	1	9	3	1?
– Mixture including parts of subdivisions above and below				3						1	1	1	1	2?	
– Cave pearl and bone layer interfingering with flawstone (Levels 7,8)	107-c.109	2		4	2	1		4		4	11		12	3	
Total		4+1?		15	2	1		14	1	20	27	7	27	10+2?	2?
Brownish earthy layer (Level 9) – top (including Hearth 1)	c.109- 131	2	1	3	2		1	8	2	8	9		2	16	3
	131- 141	5		2+1?				8	2	4	5	1	1	7	4
Total		7		5+1?	2		1	16	4	12	14	1	3	23	7
– upper middle	141- 151	5		2+1?		1	1?	7	4	5	4	1		6	5
	151- 161	3						5	3	3	3			5	3
	161- 171	6		1?	2	1		6+1?	4	5	3	1	1	6	2
Total		14		2+2?	2	2	1?	18+1?	11	13	10	2	1	17	10
– lower middle	171- 181	5			2			7	2	3	5	1?	1	4	4+1?
	181- 191	4						5	1	3	3			3	4
	191- 201	4+1?			2			7	4	6	4	1	3	9	5+1?
	201- 211	4	1			1		5	3	4	2	1?	2	6	3+1?
	211- 221	5		1	2			7	2	5	7	1+1?	2	7	4+1?
	221- 231	3	1		1	2		4	2	4+1?	3		1	7	8
	231- 241	5			1			8	3	7	8		5	12	6
17400 ± 350	241- 251	5			2+1?	1		7	2	4	8		3	7+1?	2+2??
	251- 261	5			1	1		6	1+1?	3+1?	5	2		7	3
Total		40+1?	2	1	11+1?	5		56	20+1?	39+2?	44	4+2?	17	62+1?	39+6?
– bottom (including small test pit in SE corner of trench)	261- 271	3			3	1		5	1	5	6	2	1	9	2
	271-c.290	2			1	3		7	1	6	7		2	5	2
Total		5			4	4		12	2	11	13	2	3	14	4
(Bottom of excavation, but possibly not of Brownish earthy layer, Level 9)	c.290														
Unexcavated deposit	at least 400														

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recovered from excavations made in Devil's Lair in 1972 and 1973

TRENCH 6

Petrogale not specifically identified	Macropus eugenii	Macropus irma	Macropus fuliginosus	Setonix brachyurus	Hydromys chrysogaster	Pseudomys albocinereus	Pseudomys occidentalis	Pseudomys shortridgei	Pseudomys praeconis	Notomys not specifically identified	Rattus fuscipes	Rattus not specifically identified	Muridae, total	Mocroderma gigos	Nyctophilus timoriensis	Nyctophilus geoffroyi	Eptesicus pumilus	Cholinolobus gouldii	Pipistrellus tasmaniensis	Tadarida australis	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume of major stratigraphic division excavated, cu. m	Incidence of vertebrate animals, individuals per cu. m	Depth below cave datum in line of section, NW corner of trench, cm
			1?								4	5	5								2	2				12	0.30	40	54– 77
1			1	1							11	16	16								3	1							77– 87
2	1+1?	1	5								5	7	9								12	2	p						87–c. 97
	1	1	?								1	2	2								4	1	p						
4		3	1	24							5	12	12							1	18	5	p						97–c.107
	1		1	1							1	1	1								3	1	p						
	3	2	3	25							3	9	9							1	17	3	p						107–c.109
7	6+1?	7	5	57							26	47	49							2	57	13	5			340	0.45	720	
3	3	4	6	9		1				1	4	8	10								4	8	p						c.109– 131
5+1?	1+1?	1?	2	4	1	1			1	4	3	4	14								4	30	p	1?					131– 141
8+1?	4+1?	4+1?	8	13	1	2		1		5	7	12	24								8	38	2	1?		209	0.48	435	
6+1?	1		2	3			1			3	5	1	15								2	28	p						141– 151
4		2+1?	2	2						1?			2								3	12	p						151– 161
6		1	2	2				3		2	2		10								3	23	p						161– 171
16+1?	1	3+1?	6	7				3	·1	5+1?	7	1	27								8	63	3		c	242	0.45	540	
3+1?			4	1?		1		2				1	7								3	11	p						171– 181
5			2	1						1?			2									5	p						181– 191
5		1+1?	4			1		1?		1	1	3	6								4	6	p						191– 201
2	1		1	1?		2				1?	2	3	8								4	13							201– 211
7		3	3	3		2			1	2+1?	6	2+1?	15								5	13	p						211– 221
	1?	1+1?	2	3					1		2	4+1?	6								2	7	p	1					221– 231
6+1?	2	1	5	3		2			1		4	11	15								3	10	p						231– 241
7		1	5	5					1	3	4	7	12								2	7	p						241– 251
3+1?		2	2	3		1				1	1	4	7								2	6	p	1					251– 261
38+3?	3+1?	9+2?	28	18+2?		9		6+1?		7+3?	20	35+2?	78								25	78	8	2		661	1.35	490	
5		2?		7		1				1	5	3	9								2	9	p						261– 271
3		2	3	4		1?		1			3	14	16								1	6	p						271–c. 290
8		2+2?	3	11		1+1?		1		1	8	17	25								3	15	2			148	0.24	620	

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TRENCH 5

Stratigraphic divisions and subdivisions with radiocarbon dates – yr B.P.

Stratigraphic division	Radiocarbon (yr B.P.)	Depth below cave datum in line of section, NW corner of trench, cm	Dasyurus geoffroii	Phascogale tapoatafa	Antechinus flavipes	Sminthopsis murina	Sarcophilus harrisii	Thylacinus cynocephalus	Isoodon obesulus	Perameles not specifically identified	Trichosurus vulpecula	Pseudocheirus peregrinus	Cercartetus concinnus	Potorous tridactylus	Bettongia penicillata	Bettongia lesueur
Floor of cave / Dark earthy layer		56 / 56–67	1	1	1	2			1		1	2	1	1?	3	
Flowstone complex	12050 ± 140	67– 78	1			3	3	1	4		5	9	1	4	5	
Mixture including parts of divisions above and below			2		1			1	3		1	3		1	2+1?	1?
First orange brown earthy layer – top	11960 ± 140	78– 95	3		2	3			3	1	3	4	1	3	5	2
		95– 101	2	1					3	1	3	3		·	2	2
Total			5	1	2	3			6	2	6	7	1	3	7	4
– upper middle		101– 111	1						2		1	2		1?	5	1
		111– 121	2						3	1	1	1			2	2
Total			3						5	1	2	3		1?	7	3
– lower middle		121– 141	5+1?			2			8	4	5	6		1	8	6
		141– 161	2						4		1	3		1	6	2+1?
		161– 171	1						1	1	3	2	1		8	3
		171– 181	1						1	1	1	3		1	2	2
Total			9+1?			2			14	6	10	14	1	3	24	13+1?
– bottom		181– 201	2					1	3		2	1		1	2	1
	19000 ± 250	201–c.212	1						1	1	1	3		1	1	1
Total			3					1	4	1	3	4		2	3	2
Laminated layer		c.212														
Light earthy layer		212– 220							1		1	1		1	1	
	19250 ± 900	220–c.231							2		1	1			1	1?
Total									3		2	2		1	2	1?
Banded layer		c.231														
Second orange brown earthy layer		231– 245	1						3		1	1		1	2	1
(Bottom of excavation, but not of Second orange brown earthy layer)		245														

TRENCH 2

(Upper part of deposit removed prior to 1972)

Stratigraphic division	Radiocarbon (yr B.P.)	Depth, cm	Dasyurus geoffroii	Phascogale tapoatafa	Antechinus flavipes	Sminthopsis murina	Sarcophilus harrisii	Thylacinus cynocephalus	Isoodon obesulus	Perameles not specifically identified	Trichosurus vulpecula	Pseudocheirus peregrinus	Cercartetus concinnus	Potorous tridactylus	Bettongia penicillata	Bettongia lesueur
(Pit 2 fill, lower part only)									1	1	1	1			1	2
First orange brown earthy layer – bottom		184– 199	1			1			3	1	1	1			2	1
		199– 209	1			1?			2	1	1	1				1
		209– 219	1						1		1	1		1	2	
		219–c.223									1	1			2	
Total			3			1+1?			6	2	4	3		1	6	2
Lithified band with charcoal		c.223														
Light earthy layer		223– 237	1						1		1	1			1	
Second orange brown earthy layer	20400 ± 1000	237–c.267	1	1					2	2	1	2		1	1	
Lithified layer, prominently laminated		c.267– 296	1			2			1		1	2	2		1	
Third orange brown earthy layer		296– 316	1			1										
Banded layer		316–c.339	1			3			2	2		2	1			1
Charcoal rich band / Fourth orange brown earthy layer	24600 ± 800	c.339 / 340– 346	1			1?			1			1				2
(Bottom of excavation, but possibly not of Fourth orange brown earthy layer)		346														
Unexcavated deposit		at least 460														

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recovered from excavations made in Devil's Lair in 1972 and 1973

Petrogale not specifically identified	Macropus eugenii	Macropus irma	Macropus fuliginosus	Setonix brachyurus	Hydromys chrysogaster	Pseudomys albocinereus	Pseudomys occidentalis	Pseudomys shortridgei	Pseudomys praeconis	Notomys not specifically identified	Rattus fuscipes	Rattus not specifically identified	Muridae total	Macroderma gigas	Nyctophilus timoriensis	Nyctophilus geoffroyi	Eptesicus pumilus	Chalinolobus gouldii	Pipistrellus tasmoniensis	Tadarida australis	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume of major stratigraphic division excavated, cu. m	Incidence of vertebrate animals, individuals per cu. m	Depth below cave datum in line of section, NW corner of trench, cm
	1?	1		1						1	2	1	3								3	5		1		29	0.17	170	56– 67
	1	1+1?	2	6		2					5	4	7								8	4	p			67	0.18	370	67– 78
2	1		1	3								1	1								2	2	p						
1	3	1	1	5			1?				1	1	3								1	6	p						78– 95
2			1	1									1								1	3	p						95– 101
3	3	1	2	6			1?				1	1?	4								2	9	2			79	0.28	355	
2	1		2	1							1		1?									7							101– 111
2			1	1						1	1		2									4							111– 121
4	1		3	2						1	2		3									11					49	0.24	205
6	1		1	4		3	1+1?			1	2	4	11								3	13	p						121– 141
4+1?	1		1										1								3	5	p						141– 161
2																					1	3	p						161– 171
4		1	1			1						1	2								1	2	p						171– 181
16+1?	2	1	2	5		4	1+1?			1	2	5	14								8	23	4			174	0.66	265
3		1	1								1	1	1									3							181– 201
1			1								1	1	1								1	1							201–c.212
4		1	2								2	2	2								1	4				37	0.30	120
1		1	1	1							1	1	1								1								212– 220
			1										2																220–c.231
1		2	1	1							1		3								1					19	0.15	130
1			1+1?							1			2								1	2				18	0.11	160	231– 245

Petrogale not specifically identified	Macropus eugenii	Macropus irma	Macropus fuliginosus	Setonix brachyurus	Hydromys chrysogaster	Pseudomys albocinereus	Pseudomys occidentalis	Pseudomys shortridgei	Pseudomys praeconis	Notomys not specifically identified	Rattus fuscipes	Rattus not specifically identified	Muridae total	Macroderma gigas	Nyctophilus timoriensis	Nyctophilus geoffroyi	Eptesicus pumilus	Chalinolobus gouldii	Pipistrellus tasmoniensis	Tadarida australis	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume excavated, cu. m	Incidence	Depth, cm
1			1				1?				1		2								1	1	p			14	0.02	700	
1			1	1								1										1							184– 199
1		1	1	1																		2	p						199– 209
1						1?						1	1								1	1	p						209– 219
1																						1							219–c.223
4		1	2	2			1?						2								1	5	2			48	0.25	190
		1									1	1								2	p				10	0.07	140	223– 237
2			1	1		1?							2								2	2		1		22	0.15	150	237–c.267
			1	1	1	1					3	9	11								1	1				25	0.13	190	c.267– 296
1?		1	1	1						1	1	2	4									1				9	0.09	100	296– 316
	1	1	1		5	1	3			2	6	5	17								2	2				36	0.10	360	316–c.339
		1	1	1	2	1					2	2	5								2	1				16	0.03	530	340– 346

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TRENCH 7

Stratigraphic divisions and subdivisions	Depth below cave datum in line of section, cm	Dasyurus geoffroii	Phascogale tapoatafa	Antechinus flavipes	Sminthopsis murina	Sarcophilus harrisii	Thylacinus cynocephalus	Isoodon obesulus	Perameles not specifically identified	Trichosurus vulpecula	Pseudocheirus peregrinus	Cercartetus concinnus	Potorous tridactylus	Bettongia penicillata	Bettongia lesueur
	(NW corner of Trench 7c)														
Floor of cave / Dark earthy layer (A,B,C, A under C,E, A under E)	69 / 69–c. 79	5		7+1?	4	1		9	1	6+1?	7+1?	4	6+1?	6	4
Mixture including parts of divisions above and below				2				1		2			1		
Flowstone complex – D	79–87	1+2?					1?	3		3	1		3	3	1
– G,H,I	87–c. 90	2		4				7		10	8+1?		5	7	1
– J	c. 90	2		4	6			6	1	6	11	2	3	5+3?	1+2?
– K (including Occupation Floor 1, Dortch 1974)	c. 91				1					1	1			1	
– L		2	1?	5	3			9		7	5+1?	3	5+1?	3+2?	1+1?
– Mixture including parts of subdivisions above															
Total		7+2?	1?	13	10		1?	25	1	27	25+2?	5	16+1?	19+5?	4+3?
Mixture including parts of divisions above and below		1		1				2		3	3		1?	3	
First orange brown earthy layer – top – Hearth 2	92–93	2		2	7	1		3		3	5	2	5	3	2+1?
– M (including orange and brown mottled portions)	93–110	9	2	1	11	1+1?		23	8	16	16	2	4+1?	26	9+1?
– Hearth z		2						3			2		1	1	1?
– HP					1?			1		1	1			1	
– "below HP"		1						1			1			1?	
– MM (pale friable coarse grained layer)	110–c. 115	3			2+2?	2		4	2	3	4			5	4
– Hearth y					1?			1	1	1	1	1	1	2	1
– Sub MM		2			2	1?		2	2	1	1	1	1	2	1
Total		20	2	3	22+4?	4+2?		38	13	25	31	6	12+1?	40+1?	17+3?
(Bottom of excavation but not of First orange brown earthy layer)	c. 115														

TRENCH 8

Stratigraphic divisions and subdivisions	Depth below cave datum in line of section, cm	Dasyurus geoffroii	Phascogale tapoatafa	Antechinus flavipes	Sminthopsis murina	Sarcophilus harrisii	Thylacinus cynocephalus	Isoodon obesulus	Perameles not specifically identified	Trichosurus vulpecula	Pseudocheirus peregrinus	Cercartetus concinnus	Potorous tridactylus	Bettongia penicillata	Bettongia lesueur
	(NW corner of Trench 8_7)														
Floor of cave / Dark earthy layer (A,C, A under C,E, A under E)	79 / 79–c. 109			2				1	1	2				1	
Mixture including parts of divisions above and below		3		7+2?	5	1		6	1	5+1?	5	4	5	4	1+1?
Flowstone complex – F (gypsum)	c. 109–110	1						1		1	1		1	1	
– K (including Occupation Floor 1, Dortch 1974)	110–?	1			8	2		4	2	4	3	3	3	4	2
Total		2			8	2		5	2	5	4	3	4	5	2
First orange brown earthy layer – top – Hearth 2		2			6	5+2?		3	1	4	3		2	4	3
(TRENCH 8_2 only) – M	116–122	1			7	5	1	3	2	2	2	1	1	2	1
– MM (pale friable coarse grained layer)	122–128				3			1	1	1		1			1
– Hearth y	128–129	2			4	2		2	1	2	1	4		3	1
– Mixture including parts of subdivisions above					1	3		1	1	1	1	1?		1	1
– Hearth y plus Sub MM		1						1	1	1	1			1	1
– Sub MM	129–c. 136	1			1			2	1	1	2		1?	1	1
Total		7			18	19+2?	1	13	7	12	10	6+1?	3+1?	12	9
– Mixture of subdivisions above and below					1?			1			1			1?	
– upper middle – N	c.136 / 136–149	1	1	1	3			5	1	2	3		1	3	3
– O	149–151	2			1			3	1	1	1	2		1	1
– P	151–161	2			2		1	3	2	2	2	1	1	3	3
Total		5	1	1	6		1	11	4	5	6	3	2	7	7
(Bottom of excavation but not of First orange brown earthy layer)	161														

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recovered from excavations made in Devil's Lair in 1972 and 1973

Petrogale not specifically identified	Macropus eugenii	Macropus irma	Macropus fuliginosus	Setonix brachyurus	Hydromys chrysogaster	Pseudomys albocinereus	Pseudomys occidentalis	Pseudomys shortridgei	Pseudomys praeconis	Notomys not specifically identified	Rattus fuscipes	Rattus not specifically identified	Muridae total	Macroderma gigas	Nyctophilus timoriensis	Nyctophilus geoffroyi	Eptesicus pumilus	Chalinolobus gouldii	Pipistrellus tasmaniensis	Tadarida australis	bird	lizard	snake	frog	fish	Total vertebrate individuals	Volume of major stratigraphic division excavated, cu. m.	Incidence of vertebrate animals, individuals per cu. m.	Depth below cave datum in line of section, cm.
																													(NW corner of Trench 7c)
6	1	1	3	8		5	3			1+1?	16	12	29			1			1+1?		11	7+1?	p			135	0.19	710	69 / 69-c. 79
1				1								1	2								2	2	p						
2	1	1?	1	4								2	3								2	2	p						79- 87
4		1+1?	4	14		1					6	10	14	1	1?						6	6	p	1?					87-c. 90
1	2	1	3	7+1?		4					4	5	13					1?			11	7 / 1	p						c. 90 / c. 91
3	2	2?	3	7						1?	9	8	16						1		10	8	p						
10	5	2+4?	11	32+1?		5				1?	19	25	46	1	1?			1?	1		29	24	4	1?		351	0.37	950	
1	2		1	2		1					1	3	4								4	2	p						
1	1	1+1?	2	4		4				2	6	6	14	1	1?		1	1	1?		9	3	p						92- 93
10	8+1?	2+1?	8	9		12	3+1?			11+1?	22	22	54			1		1			19	36	p						93- 110
1			1	1								1	1									2							
1			1																			1							
1										1?			1								2	4	p						
2	1	1	1	3		4				3	6	8	16			1					2	19							110-c. 115
1	1	1	.			3				3	1	1	7								1	7							
1+1?	1	1		1		4				3	4	2	12								2	11							
18+1?	12+1?	6+2?	13	18		27	3+1?			22+2?	39	40	105	1	1?	2	1	2	1?		35	83	3			549	0.58	950	
																													c. 115

Petrogale	M. eugenii	M. irma	M. fuliginosus	Setonix	Hydromys	P. albocinereus	P. occidentalis	P. shortridgei	P. praeconis	Notomys	R. fuscipes	Rattus n.s.i.	Muridae total	Macroderma	N. timoriensis	N. geoffroyi	Eptesicus	Chalinolobus	Pipistrellus	Tadarida	bird	lizard	snake	frog	fish	Total vert.	Volume	Incidence	Depth
																													(NW corner of Trench 8₁)
	1?			1							3	5	5								5	2				21	0.31	70	79 / 79-c. 109
3+2?	3	1+1?	2	8		5	1			2+1?	19	25	34	1			1	1			9	5	p						
2		1	1	3			1	1?			3	4	6								2	1	p						c. 109- 110
1	1	2	2	6		2	1			1	7	14	18			1?		1+2?	1		7	4	p	1	1				110- ?
3	1	3	3	9		2	2	1?		1	10	18	24			1?		1+2?	1		9	5	2	1	1	108	0.05	2000	
2	1	1	2	3		3	3			3	7	15	24						3		6	9	p						
																													(NW corner of Trench 8₂)
1		1	1	2		4	1			4	8	9	18					1	2		6	4	p	1					116- 122
1						4	1			3	1	3	11								1	4							122- 128
1	1	1	1	2		6	1			6	5	13	26						1		4	8	p	1					128- 129
1		1		3		3	2	1?		2	4	4	11	1							2	5	p						
1			1?	1		1	1			1	1	1	4								2	3							
1			1	1		3					1	1	4								1	3							129-c. 136
8	2	4	5+1?	8		24	9	1?		19	26	46	98	1				1	6		22	36	4	2		319	0.29	1100	
						1							2									2							
3		1	2	1		2	1			1	3	2	7								1	36	p						c. 136 / 136- 149
1		1	1	1?	i	3	1	1?			2	4	10								1	44	p						149- 151
1		1?	1	1		2	1			1	2	2	6								4	24	p						151- 161
5		2+1?	4	2+1?	1	7	3	1?		2	7	8	23								6	104	3			210	0.18	1200	
																													161

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Appendix 2

Records forming the basis for the modern mammal fauna of the Devil's Lair district

by A. Baynes

The evidence presented here depends upon unpublished research on the distributions of most south western mammal species. Some have not yet been fully covered, and their status is correspondingly less certain.

Unless otherwise stated all specimens referred to are in the collections of the Western Australian Museum. Those in the modern mammal collection are distinguished by a simple number, usually with the prefix M; vertebrate palaeontological collection specimens quoted have numbers divided by two fullstops, and no letter prefix.

Mammals listed in Table 3, confidently included in the modern fauna

Dasyurus geoffroii. Three specimens (M1839, M1852, M1861) in the modern mammal collection of the W.A. Museum were obtained in 1934 from Forest Grove 8 km N.E. of Devil's Lair. Two specimens (M1824, M1825) sent in from Forest Grove in the same year, and another (M1717) from Karridale 7 km south in the previous year were all discarded after registration.

Phascogale tapoataja. The closest specimen was obtained from Forest Grove in 1933. Other single records from within 20 km of Devil's Lair are M2032 from Forest Grove in 1936 (discarded), M2270 from Witchcliffe in 1938, M2711 from East Witchcliffe in 1946 (discarded), M5090 from Kudardup in 1962, and M7944 from Augusta in 1967. In addition eight *P. tapoataja* have been recorded from Margaret River; those for which the accession number as well as the year is in brackets were discarded: M1588 (1931), (M2707, 1946), (M2911, 1952), M4028 (c. 1960), M4293 (c. 1960), M4534 (c. 1960), M4569 (1961), M6901 (1966).

Sminthopsis murina. A specimen (M206) was obtained in the "Caves District" in 1915, and three others (M1171, M1642, and M2059) were sent in from Forest Grove in 1929, 1932 and 1936 respectively.

Tarsipes spencerae. A specimen (M1250) was sent in to the W.A. Museum in 1930 from Group 75 which is probably east of Forest Grove rather than near its postal address at that time, which was Karridale. Either way the specimen probably originated within 10 km of Devil's Lair. Another specimen (M2397) obtained from Karridale in 1940 was not kept.

Trichosurus vulpecula. A specimen (M112) from near Mammoth Cave was registered in 1914 but discarded; another (M6583) was collected at the same locality in 1965. A specimen (M224) was obtained from Margaret River in 1915.

Pseudocheirus peregrinus. Only a single modern specimen (M5835) has been found near Devil's Lair. It consists of a jaw picked up on the surface from near Lake Cave, about 8 km N. of Devil's Lair, in 1963. Shortridge (1910) reported that the species was fairly plentiful near Margaret River at the time of the Balston Expedition of 1904-1907. He collected several at Burnside. Remains of *P. peregrinus* are also moderately common on the surface in other caves near Devil's Lair.

Cercartetus concinnus. This species is represented as a modern mammal in the immediate area by a single record, M1715 from Forest Grove, sent to the Western Australian Museum in 1933 but subsequently lost. Another (M2217) was obtained from Margaret River in 1937. Its remains are found on the surface of cave deposits in the region. Also it was represented in a small cave deposit at Turner Brook, 14 km S. of Devil's Lair which was radiocarbon dated at 430 ± 160 years B.P. (Archer and Baynes 1972).

Bettongia penicillata. A series of specimens (M17-M23) were obtained near Mammoth Cave in 1912. Of these M17 and M20 are still represented by specimens in the W.A. Museum. Two (M1084, M1086) were obtained from Karridale in 1928, and another two (M1340, M1351) were sent in from Karridale in 1930. M1351 was discarded.

Macropus fuliginosus. A modern skull (M2364) was obtained from Calgardup Brook in 1939 and another (M2389) sent in to the W.A. Museum in the same year from Witchcliffe. Remains of the species are common on the floors of many other caves in the area around Devil's Lair. Kangaroos of this species were seen frequently during field work at Devil's Lair in 1973.

Setonix brachyurus. Modern specimens were sent in from Karridale as follows: M1121, M1125 (1929), M1402 (1931), and M1765 (1933). The catalogue indicates that another (M115) merely labelled as from the Margaret River district, was collected near Mammoth Cave in 1914. Specimen 8924 originated from Margaret River in 1907. Surface specimens of the species are common in caves throughout the Cape Leeuwin-Cape Naturaliste region. *Setonix brachyurus* was collected at Augusta by John Gilbert (Thomas 1888).

Hydromys chrysogaster. A specimen (M1685) sent in from Forest Grove in 1933 was discarded, but three others (M6576, M6580-1) were collected alive in Mammoth Cave in 1965. Specimen M7 was sent in from the Margaret River district in 1912, and M221 was obtained from the same area in 1915 but discarded.

Rattus fuscipes. This species is today common in the immediate vicinity of Devil's Lair, e.g. M8166. There is a modern specimen (44.2.15.36) from Augusta registered in the British Museum (Natural History) in 1844 (Taylor and Horner 1973): this was probably collected by John Gilbert.

Mammals listed in Table 4, probably part of the modern fauna

Eight of the twelve species in this group are represented by specimens collected alive in the general area.

Antechinus flavipes. A specimen (M2037) was obtained in 1936 from Rosa Brook about 22 km N.N.E. of Devil's Lair. Also species is abundant in the fossil fauna from the small deposit at Turner Brook (Archer and Baynes 1972). *A. flavipes* remains are present on the surface in several caves near Devil's Lair.

Isoodon obesulus. Five specimens have reached the W.A. Museum from the Margaret River district at various times: M226 (1915), M4522 (1959), M4466 (1960) M7580 (1966), M7626 (1967). The species was also collected near Margaret River by Shortridge (1910). Its remains are abundant on the surface in a number of caves near Devil's Lair, and it was present in the small deposit at Turner Brook (Archer and Baynes 1972).

Potorous tridactylus. Although this species has not been collected as a live animal near Devil's Lair its remains are very common on the surface in caves in the area. It seems likely that it was present as a member of the modern fauna around Devil's Lair. Information obtained by Shortridge (1910) from Aborigines also suggests that it was present in the Margaret River dis.rict during the last century.

Macropus irma. In some ways this species represents the greatest problem of interpretation because specimens collected alive in the region may falsely suggest the species to have been a member of the modern fauna around Devil's Lair. A specimen (M458) was obtained from Augusta in 1920, and another (M8335) along the Brockman Highway between Augusta and Margaret River in 1968. Perry (1971) includes *M. irma* in a list of species frequently seen along the lower Blackwood River in 1919. Against this evidence is the fact that although remains of the species are known from caves near Devil's Lair the specimens have all undergone some chemical alteration, suggesting age. Most originate from caves known to contain material of considerable antiquity. It is possible that *M. irma* reinvaded the area near Devil's Lair after the first felling of the forests last century.

The three rodent species in Table 4 were all present in the deposit at Turner Brook (Archer and Baynes 1972). Both *Pseudomys shortridgei* and *Rattus tunneyi* were abundant in the deposit; *Pseudomys praeconis* was only represented by 3 specimens in a total of about 650. However, this low relative abundance of *P. praeconis* in a cave deposit fauna is typical of this species in the southern part of its range (A. Baynes, unpublished observations).

Nyctophilus timoriensis. The modern specimens collected nearest to Devil's Lair were obtained about 60 km away: M36 from Nannup in 1913, and M1247 and M1248 from Wonnerup in 1929. However, the

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total number of modern specimens in the collection is quite small. The species is included in Table 4 on the record of its presence in the deposit at Turner Brook (Archer and Baynes 1972).

Many bat species are among the mammals not yet fully covered in the survey of distributions, but the modern mammal collection of the Western Australian Museum includes specimens of four species collected near Devil's Lair. One specimen with its year of capture is quoted for each: *Nyctophilus geoffroyi* M6584 near Strongs Cave just to the west of Devil's Lair in 1965, *Eptesicus pumilus* M4183 Boranup about ½ km east of Devil's Lair in 1961, *Chalinolobus morio* M3788 in Mammoth Cave 10 km north of Devil's Lair in 1959, and *Pipistrellus tasmaniensis* M4182 from Boranup in 1961.

Canis familiaris. Shortridge (1936) collected five specimens of Dingo from Margaret River during the Balston Expeditions of 1904-07 and Perry (1971) includes it in the list of species frequently seen on the Lower Blackwood River in 1919. The W.A. Museum has only a single modern specimen from the Margaret River district, M4204 collected in 1953. However, the locality of even this one is suspect. The species is abundantly represented by remains on the surface of deposits in caves near Devil's Lair. One cave has been named Dingo Cave because so many skulls have been recovered from it.

Mammals listed in Table 5, possibly forming part of the modern fauna

Macropus eugenii. This species is placed here mainly because of a lack of fossil specimens of young appearance from caves near Devil's Lair. All those known originate from caves which include material of considerable antiquity. They are generally encrusted or appear to have undergone chemical alteration. The closest record to Devil's Lair of *Macropus eugenii* taken alive is the specimens collected by Shortridge (1910) at Ellensbrook about 30 km to the north. W. D. L. Ride possesses copies of the data on the labels of five of these specimens which are in the British Museum (Natural History). The label attached to the skin of No. 6.9.1.32 bears the following note "*Macropus eugenii* does not seem to occur to the south of Margaret River on the coast (according to natives)". Ride (pers. comm.). The author of the note was probably Shortridge. There are other specimens from this general area in the W.A. Museum modern mammal collection. One from Cape Naturaliste about 65 km north of Devil's Lair consists of only a skin to which is attached a Tunney collecting label bearing the number 06 and the locality, but no date. It was probably collected between 1900 and 1910. Three other specimens (12860-2) were collected at Lake Muir about 140 km E. of Devil's Lair in 1912.

Chalinolobus gouldii. The nearest records of modern specimens are from 55 km from Devil's Lair: M8391 at Busselton in 1969 and M10935 from Darradup in 1973.

Tadarida australis. The nearest record is M5420 collected in 1963 at Donnelly River Mill, about 75 km E. of Devil's Lair.

Mammals listed in Table 6, not present in the modern fauna of the Devil's Lair district but recorded in the fossil fauna.

It is necessary to consider the records of one of the species included in Table 6.

Petrogale sp. It is unlikely that any species of *Petrogale* was present in the modern fauna of the Devil's Lair district. Fossil specimens are known from a number of caves near Devil's Lair, but all originate from deposits which are known to include specimens of considerable age, and most appear to have undergone some chemical alteration. In addition there is one specimen which must be discussed in detail. It is a skull of *Petrogale* sp., at present in the vertebrate palaeontological collection (69.6.62), but formerly in the modern mammal collection (M114). The catalogue indicates that M114 is a skull of *Setonix brachyurus* from "Mammoth Cave, Margaret River" collected by L. Glauert in April 1914. Specimen M115 is a skin and skull of *Setonix brachyurus* with the same locality data as M114. Skull 69.6.62, still bearing the number M114, retains the remains of dried flesh (e.g. the left eardrum) it also shows starred fractures of the cranium behind the left orbit. On this evidence it seems likely that the specimen was collected as a live animal, probably with a shot gun, and that it is not a fossil. The nearest locality from which living specimens of a *Petrogale* sp. have been recorded is Dale River near Beverley (Shortridge 1910). This is about 240 km N.N.E. of Mammoth Cave. When this gap is considered in conjuction with the absence of young fossil material from caves near Devil's Lair, it appears likely that specimen 69.6.62 is the result of misassociation of specimen and data during preparation or storage.

Appendix 3

Investigation of degree of overestimation inherent in our methods of obtaining "minimum numbers" of individuals

The entries in Appendix 1 represent our estimated "minimum number" of individuals for each taxon for each stratigraphic unit specified. In the case of Trench 6, however, excavation was made by 2 cm spits from 109 cm to 271 cm, but for convenience in tabulation, we show the data grouped into 10 cm intervals. Grouping was made by adding the 2 cm spit records for each taxon.

In order to investigate the maximum degree of overestimation of "minimum numbers" of individuals inherent in our methods, we chose the 211 cm to 271 cm interval in Trench 6 because it both contained sufficient numbers of specimens of very large and very small animals, and appeared to be a stratigraphic continuum. This interval was excavated in horizontal spits 2 cm thick in what we later judged from the sections and from our observations as excavation progressed to be a continuum of gently dipping sediments. Not only were our spits very small but they transgressed the dipping bedding planes, so that different beds might be represented in the same spit.

We assembled all the bone material of three species, catalogued or otherwise, which was admitted to our analysis from this 211 to 271 cm interval in Trench 6. The first of these species was one of the smallest sized mammals represented, *Sminthopsis murina*, the second was a species of intermediate body size, *Pseudocheirus peregrinus* and the third was the largest species (with the possible exception of man) so far recorded in the deposit, *Macropus fuliginosus*. In each case, the number of individuals was estimated without regard to depth, as though complete vertical mixing had occurred. This was in contrast to the assumption on which the appendix tables were prepared, namely that no vertical mixing had occurred between 2 cm spits. It is to be expected that the true number of individuals represented in the deposit would lie between these two extremes. The degree of overestimation in the appendix tables would be expected to be least for *Sminthopsis*, intermediate for *Pseudocheirus* and greatest for *M. fuliginosus* because a small thickness of sediment would completely cover all *Sminthopsis* bones, most *Pseudocheirus* bones, but few *Macropus fuliginosus* bones. Vertical mixing would be greatest for this last named species because larger bones would be more likely to be dislodged by scuffling human or other feet, whereas small bones would be more likely to be trodden in.

The number of individuals of *Sminthopsis murina* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 10. When we considered the specimens as a single sample

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irrespective of depth, there proved to be 5 left dentaries, 6 right dentaries, 2 left maxillae and 2 femora. Some of these were incomplete, but no two tooth bearing fragments from the same quarter could have represented the same animal. So on these grounds at least 6 individuals were represented. Appreciable tooth wear was discernible on 3 of the left dentaries but not on any of the 6 right dentaries, so that at least 3 aged animals and 6 young animals must have contributed to the sample, making 9.

Of the 29 spits involved, only two pairs of adjacent spits contained *S. murina*. These pairs and the other 6 spits containing *S. murina* were separated from one another by at least 2 cm and up to 8 cm. On depth grounds alone at least 8 individuals might be expected.

Thus it would appear that our methods did not result in great overestimation of the numbers of individuals of *S. murina*. By extrapolation to other depth ranges and other very small species, we suggest that the numbers in the appendix tables are not greatly overestimated.

The specimens of *S. murina* involved in this test were 73.8.638, 746, 802, 892, 927, 958, 969; 73.9.24, 41, 37; 73.12.309, 310.

The number of individuals of *Pseudocheirus peregrinus* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 37. By assembling the specimens irrespective of depth, we could demonstrate the presence of only 21 individuals, the key anatomical structure in this case being left dentary fragments with third molars or their alveoli. Thus our methods may overestimate the numbers of individuals of this, and presumably other animals of intermediate size, to an appreciable extent. In this case we had no guide from depth considerations because all but one of the 29 spits contained *P. peregrinus*.

The specimens involved were 73.8.584, 585, 602, 625, 653, 654, 671, 713, 732, 751, 781, 782, 808, 809, 826, 855, 856, 876, 877, 895, 909, 910, 930, 931, 948, 962, 972, 988; 73.9.18, 28, 47, 48, 67, 75, 89; 73.12.332, 339, 343.

The number of individuals of *Macropus fuliginosus* recorded in the Appendix 1 tables between 211 and 271 cm in Trench 6 is 17. From the specimens assembled as one sample, irrespective of depth, we could demonstrate the presence of only 6 individuals, the key anatomical structure in this case proving to be left upper first incisor teeth.

In order to judge the possible effect of excavating by 10 cm instead of 2 cm spits, we then assembled the *M. fuliginosus* specimens from the 211 to 271 cm interval in Trench 6 in groups from 211 to 221 cm, 221 to 231 cm, and so on. If we had in fact excavated Trench 6 in these 10 cm spits, we would have recorded only 9 individuals of *M. fuliginosus*, thus probably overestimating, but much less seriously than by excavating as we did in 2 cm spits.

The *M. fuliginosus* specimens involved were 73.8.591, 608, 644, 738, 763, 793, 815, 836, 863, 883, 900, 901 917, 935, 977; 73.12.308, 333, 335, 372.

As a further check on the degree of overestimation of *M. fuliginosus*, we considered specimens from spits of about 10 cm thickness excavated from Trench 5, between 78 cm and 212 cm. We believe these range through the same major stratigraphic division as the interval from Trench 6 previously considered, though the Trench 5 sample probably represents a larger proportion of this stratigraphic division. There were 9 individuals of *M. fuliginosus* recorded for the 78 to 212 cm depth interval in Trench 5. When we assembled the specimens as a sample irrespective of depth, we could demonstrate the presence of only 4 separate individuals, with anterior molariform teeth providing the best guide to numbers in this particular sample. The specimens concerned were 73.9.354, 381, 409, 429, 430, 460, 532, 677, 703, 783; 73.12.499.

As a final check on overestimation of *M. fuliginosus*, we assembled all the material from Trench 6, not only of the categories used to assemble the data for the appendix tables but also any other post cranial material attributable to *M. fuliginosus* by reason of its size or form. Ignoring all consideration of depth or stratigraphy, we could demonstrate the presence of only 17 individuals of *M. fuliginosus*, compared with 50 estimated by adding the entries for the various stratigraphic subdivisions, as in Appendix 1.

By considering separately the major stratigraphic subdivisions of Trench 6, but using the full sample of *M. fuliginosus* rather than the partial sample on which Appendix 1 is based, and omitting stratigraphically mixed samples, we reached the following estimates of minimum numbers:—

First dark earthy layer	1	(not included in Appendix 1 tables because based on post cranial elements not admitted to our analysis)
Pale band	1	(ditto)
Flecked . . . lens	1	(ditto)
Second dark earthy layer	2	(cf. 1 in Appendix 1 tables)
Cave pearl and bone layer	2	(cf. 3 in Appendix 1 tables)
Brownish earthy layer—top	7	(cf. 8 in Appendix 1 tables)
Brownish earthy layer—upper middle	2	(cf. 6 in Appendix 1 tables)
Brownish earthy layer— lower middle	8	(cf. 28 in Appendix 1 tables)
Brownish earthy layer— bottom	2	(cf. 3 in Appendix 1 tables)

The lower middle subdivision of brownish earthy layer, for example, was excavated in 43 two centimetre spits and 1 four centimetre spit, and minimum numbers for each species estimated for each spit. The 28 *M. fuliginosus* individuals recorded in Appendix 1 for this subdivision represent the sum of the numbers recorded for each spit; this is in marked contrast with only 8 individuals estimated by treating the subdivision as though it were a discrete stratigraphic entity. (There may be some connection between the high degree of overestimation in this stratigraphic subdivision and the low degree of bias imposed by the collecting agency, implied in Table 1, but if so, we have made no study of any such connection.)

We conclude that our methods may lead to overestimation, which becomes more likely with increasing size of. the animal concerned and decreasing thickness of the excavation unit sampled.

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